

Greater Prairie-Chicken (*Tympanuchus cupido*): A Technical Conservation Assessment



**Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project**

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COVER PHOTO CREDIT

The greater prairie-chicken (*Tympanuchus cupido*) photo was provided by Robert E. Bennetts from photography in Colorado.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF GREATER PRAIRIE-CHICKEN

Status

The geographic distribution and abundance of greater prairie-chickens (*Tympanuchus cupido*) have fluctuated dramatically during the last 200 years following settlement by people of European descent, but in recent decades virtually all changes have resulted in reduced abundance and smaller, more fragmented distributions. One subspecies of the greater prairie-chicken, the heath hen (*T. c. cupido*), became extinct in 1932. A second subspecies, Attwater's prairie-chicken (*T. c. attwateri*), is federally listed as endangered and is close to extinction. The remaining subspecies (*T. c. pinnatus*) is the only subspecies found in Region 2, and it is locally extinct, threatened, endangered, or harvestable, depending on location.

Primary Threats

The major threats to greater prairie-chicken populations in Region 2 are the loss, fragmentation, and degradation of potential and occupied habitat on both private and public lands, which could occur through the following activities:

- ❖ inappropriate timing and intensity of livestock grazing
- ❖ conversion of native prairie for development and crop production
- ❖ construction of roads, utility corridors, fences, towers, turbines, and energy developments
- ❖ introduction and expansion of noxious weeds
- ❖ alteration of fire regimes
- ❖ planting of trees.

Populations in Region 2 are particularly vulnerable to changing land use practices that degrade or eliminate nesting and brood-rearing habitats. In addition, small, localized populations that are isolated from core areas may face greater risk of extinction due to a lack of connectivity.

Primary Conservation Elements, Management Implications, and Considerations

Primary conservation elements to be considered in Region 2, and in other portions of the species' distribution, include practices associated with grazing, farming, burning, and mowing of potential and occupied habitat, and the impacts of development, roads, power lines, fences, oil and gas development, tree planting/encroachment, off-road vehicles, and harvest. It is also important to recognize that drought exacerbates the impacts of these practices. The inappropriate timing and intensity of livestock grazing, in particular, can cause widespread degradation of habitat for greater prairie-chickens by homogenizing the essential heterogeneous grassland landscape that they prefer. Features associated with human development (e.g., communities, roads, land use changes, herbicides) also contribute to habitat fragmentation, alter predation dynamics, and introduce disturbance and mortality factors.

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INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service (USFS). The greater prairie-chicken (*Tympanuchus cupido*) is the focus of an assessment because one of its subspecies, the heath hen (*T. c. cupido*) is extinct; another subspecies, the Attwater's prairie-chicken (*T. c. attwateri*), is critically endangered; and the remaining *T. c. pinnatus* subspecies is extinct, endangered, or threatened in many portions of its original range (Schroeder and Robb 1993). Even though the greater prairie-chicken is still present in harvestable numbers in Region 2, some populations have declined in recent years. This assessment addresses the biology of the greater prairie-chicken (*T. c. pinnatus*) throughout its range, but in particular within USFS Region 2.

Goal of Assessment

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, research biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based on available scientific knowledge. The assessment goals limit the scope of the work to summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop specific recommendations for management of populations and habitats. Rather, it provides the ecological background upon which management would be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). Furthermore, this assessment cites previously published management recommendations and examines the success of those recommendations that have been implemented.

Scope of Assessment

The assessment examines the biology, ecology, conservation status, and management of greater prairie-chickens with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region. Some of the literature on this species originates from field investigations and planning outside the region (i.e., Minnesota, North Dakota, Wisconsin, Iowa, Missouri, Illinois, and Texas), and this document places that literature in the ecological and social context of Region 2. Some of these areas outside Region 2 are

characterized by comparable habitats and population characteristics. In fact, some of the populations are shared between states. This assessment also is concerned with reproductive behavior, population dynamics, and other characteristics of greater prairie-chickens in the context of the current environment rather than under historical conditions. The evolutionary environment of the species is considered in conducting the synthesis, but placed in a current context.

Data Used to Produce this Assessment

In producing this assessment, most attention was focused on peer-reviewed sources such as journal publications, theses and dissertations, and agency and university technical reports. The numerous references that were not peer-reviewed were not considered, except in situations where peer-reviewed information was not available. In these situations, the nature of the information was clearly acknowledged. In addition, the strength of evidence for particular ideas is noted and alternative explanations described when appropriate.

Treatment of Uncertainty

Most of the available research on greater prairie-chickens is based on correlative information. Controlled experiments at the appropriate scale are extremely difficult to conduct on species that occupy broad home ranges where there is minimal management control. Consequently, we attempted to provide details of the referenced research (such as sample sizes) so that the reader can understand some of the strengths and weaknesses of the inferences. We also attempted to avoid references that were not peer-reviewed such as magazine and newspaper articles and some agency reports. Although peer-review does not eliminate uncertainty or the possibility of error, it at least assures that the research has undergone review by other scientists.

Publication of Assessment on the World Wide Web

To facilitate use of species assessments in the Species Conservation Project, they are being published on the USFS Region 2 World Wide Web site for the Project. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More importantly, it facilitates their revision, which will be accomplished based on guidelines established by Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed prior to release on the Web. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment. Peer review of this assessment was administered by the Society for Conservation Biology, using two experts on this species or a related one.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

The recognized greater prairie-chicken subspecies vary dramatically with respect to their status. The heath hen has been extinct since 1932, and the Attwater's prairie-chicken is imperiled and considered one of the most endangered bird species in the United States (Schroeder and Robb 1993, Silvy et al. 1999, Morrow et al. 2004, Silvy et al. 2004). The remaining subspecies is considered a sensitive species in USFS Region 2. Greater prairie-chickens are legally harvested in Kansas, Nebraska, South Dakota, and Colorado (special permits required in Colorado). Greater prairie-chickens are absent in Wyoming. Outside Region 2, greater prairie-chickens are legally harvested in Minnesota and Oklahoma; harvest is not allowed in Texas, Missouri, Illinois, Iowa, North Dakota, and Wisconsin. Although greater prairie-chickens are considered a species that is 'apparently secure' by The Nature Conservancy, their distribution is extremely reduced or absent in many areas. Partners in Flight (PIF) lists the greater prairie-chicken as a 'Priority Species', places it on their 'Watch List' with multiple causes for concern across the entire range, and assigns it a 'combined vulnerability assessment' score of 17 out of a maximum possible of 20 (Rich et al. 2004).

Existing Regulatory Mechanisms and Management/Conservation Strategies

The USFS Region 2 considers the greater prairie-chicken a sensitive species based on several characteristics including distribution, population abundance and trend, habitat vulnerability and trend, dispersal capability, and demographics. The official USFS policy on "Wildlife, Fish, and Sensitive Plant Habitat Management" (Amendment number 2600-95-7; June 23, 1995) lists numerous issues that apply to the greater prairie-chicken.

FSM 2670.22 (Amendment number 2600-95-7; June 23, 1995) lists the objectives of the USFS with regard to sensitive species:

1. Develop and implement management practices to ensure that species do not become threatened or endangered because of USFS actions.
2. Maintain viable populations of all native and desired nonnative wildlife, fish, and plant species in habitats distributed throughout their geographic range on National Forest System lands.
3. Develop and implement management objectives for populations and/or habitat of sensitive species.

FSM 2670.32 (Amendment number 2600-95-7; June 23, 1995) lists the official policy of the USFS with regard to sensitive species:

1. Assist States in achieving their goals for conservation of endemic species.
2. As part of the National Environmental Policy Act process, review programs and activities, through a biological evaluation, to determine their potential effect on sensitive species.
3. Avoid or minimize impacts to species whose viability has been identified as a concern.
4. If impacts cannot be avoided, analyze the significance of potential adverse effects on the population or its habitat within the area of concern and on the species as a whole. (The line officer, with project approval authority, makes the decision to allow or disallow impact, but the decision must not result in loss of species viability or create significant trends toward Federal listing.)
5. Establish management objectives in cooperation with the States when projects on National Forest System lands may have a significant effect on sensitive species population numbers or distributions. Establish objectives for Federal candidate species, in cooperation with the USFWS or the National Marine Fisheries Service and the States.

In contrast to sensitive species, Management Indicator Species (MIS) are chosen as indicators of particular management strategies. The greater prairie-chicken has been designated as a MIS on the Nebraska National Forest and associated units (USDA Forest Service 2003). These units include the Ft. Pierre National Grassland and the Samuel R. McKelvie National Forest (**Figure 1**; Cables 2002).

Most currently occupied habitat for greater prairie-chickens in Region 2 occurs on private lands, and state and federal agencies have minimal regulatory authority to protect this species or its habitat. Consequently, addressing the problems associated

with the conservation of greater prairie-chickens will necessitate the cooperation and coordination of efforts among federal and state agencies, non-governmental organizations, and private landowners. PIF lists the greater prairie-chicken in conservation plans for the Osage Plains (Fitzgerald et al. 2000), the Dissected Till Plains (Fitzgerald and Pashley 2000), the Northern Mixed-grass Prairie (Fitzgerald et al. 1999), the Northern Tall-grass Prairie (Fitzgerald et al. 1998), and Colorado (Beidleman 2000). The greater prairie-chicken is also likely to be a major component of the plan for the Central Mixed-grass Prairie, which has not been completed yet. The International Union for Conservation of Nature and Natural Resources (IUCN)

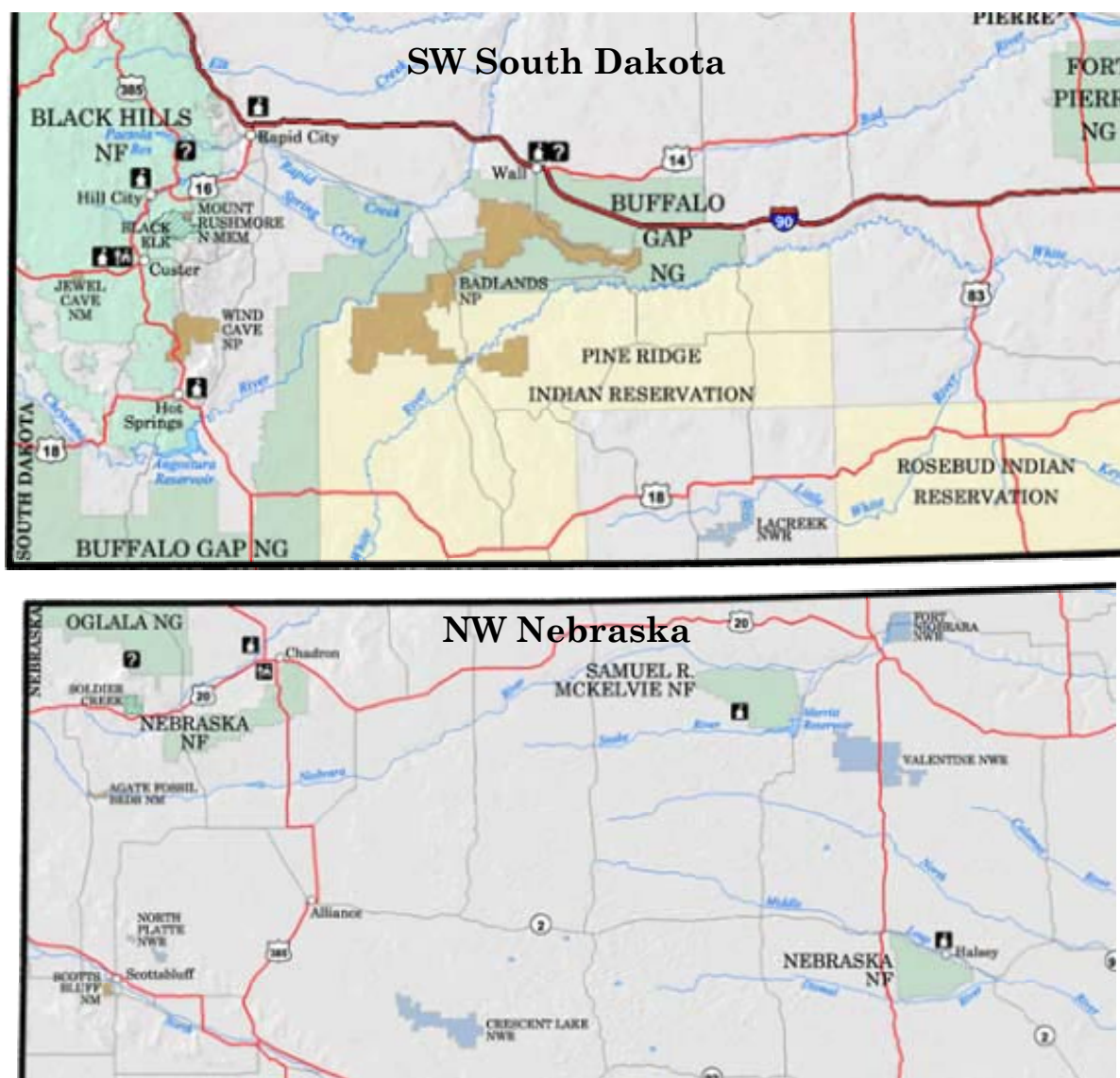


Figure 1. Location of national grasslands and forests in southwestern South Dakota and northwestern Nebraska within the Rocky Mountain Region of the USDA Forest Service.

also has produced a status survey and conservation action plan for grouse species worldwide, including the greater prairie-chicken (Storch 2000).

Biology and Ecology

Systematics and general species description

The greater prairie-chicken belongs to the Order Galliformes, Family Phasianidae, and subfamily Tetraoninae. The greater prairie-chicken originally included the lesser prairie-chicken as a distinct race (Ridgway 1873), but the lesser prairie-chicken was given its own species label (*Tympanuchus pallidicinctus*) in 1885 (Ridgway 1885). Currently, *T. pallidicinctus* and *T. cupido* are recognized as distinct species (American Ornithologists' Union 1957, 1983). However, the relatively minor differences (in appearance, habitat, and behavior) between the two species have generated debate regarding the specific classification of the lesser prairie-chicken. In general, greater prairie-chickens are slightly larger and darker than lesser prairie-chickens, and the male greater prairie-chickens have orange scarlet-edged air sacs (Giesen 1998). Aldrich and Duvall (1955:8) believed that "... no characters [of the lesser prairie-chicken] differ from those of the other prairie chickens, except in degree; thus, only a racial difference is indicated". But Aldrich (1963:537) later stated that "... the lesser prairie-chicken appears to have sufficiently separated morphological characters to be considered a distinct species by most ornithologists." Short (1967), Johnsgard and Wood (1968), and Johnsgard (1983) considered lesser and greater prairie-chickens allopatric subspecies while Sharpe (1968) suggested they were allospecies of one superspecies. However, Jones (1964) examined the behavioral and morphological characteristics of both the greater and lesser prairie-chicken and concluded that specific status of the lesser prairie-chicken was warranted, and Hjorth (1970), in a comprehensive review of the reproductive behavior of Tetraonidae, treated the greater prairie-chicken as a separate species. Examination of genetic variation among members of the genus *Tympanuchus* indicates low levels of interspecific divergence, suggesting recent speciation among the North American prairie-grouse (Ellsworth et al. 1994, 1995; Gutiérrez et al. 2000; Drovetski 2002, 2003).

Three subspecies of greater prairie-chickens are recognized: the heath hen (*Tympanuchus cupido cupido* [Linnaeus]), Attwater's prairie-chicken (*T. c. attwateri* [Bendire]) and greater prairie-chicken (*T. c. pinnatus* [Brewster]). Several observations of hybrids between greater prairie-chickens and sharp-tailed grouse (*T.*

phasianellus) have been reported (Rowan 1926, Ammann 1957, Evans 1966, Johnsgard and Wood 1968, Sparling 1980, Svedarsky and Kalahar 1980), and the rate of hybridization in Nebraska has been estimated as 0.3 to 1.2 percent (Johnsgard and Wood 1968). Hybrids between greater and lesser prairie-chickens have also been observed (U.S. Fish and Wildlife Service 2002). There is one report of a hybrid between a greater prairie-chicken and a ring-necked pheasant (*Phasianus colchicus*; Lincoln 1950). Genetic studies of the putative species in the genus *Tympanuchus* suggest a recent common ancestry; the distinctive morphological and behavioral differences observed among the different species may have rapidly evolved under pressure from sexual selection (Ellsworth et al. 1994, 1995; Gutiérrez et al. 2000; Drovetski 2002, 2003).

The genus name *Tympanuchus* comes from the Latin word *tympanum* and refers to the booming sound produced by the males during courtship. *Cupido* refers to resemblance of the pinnae feathers to "Cupid's wings" when they are raised on the sides of the neck by males during courtship. Greater prairie-chickens are a medium-sized grouse somewhat larger than lesser prairie-chickens and smaller than greater sage-grouse (*Centrocercus urophasianus*). Body mass generally averages 970 g for males and 800 g for females, but considerable variation occurs among seasons, age and sex classes, and regions (Schroeder and Robb 1993). Plumage is predominately olive-brown to buffy brown with white cross-bars on the back, wings, breast, belly, and tail (Ridgway and Friedmann 1946). The tail is short and rounded in appearance. Males have long tufts of feathers (pinnae) and orange esophageal "air sacs" on the sides of their neck; females have much smaller pinnae feathers and no air sacs (Schroeder and Robb 1993). Greater prairie-chickens may be confused with lesser prairie-chickens in areas where the two species overlap (primarily in Wallace, Logan, Gove, Trego, Scott, Lane, and Ness counties in western Kansas).

Distribution and abundance

Historical and current global distribution and abundance

Greater prairie-chickens are endemic to the grassland habitats of the central and eastern United States. Prior to settlement by people of European descent, populations inhabited the tallgrass prairies of the eastern states, with the core of the distribution centered near the intersection of Missouri, Illinois, and Iowa (**Figure 2**; Svedarsky et al. 2000). Understanding the differences between original and acquired range is

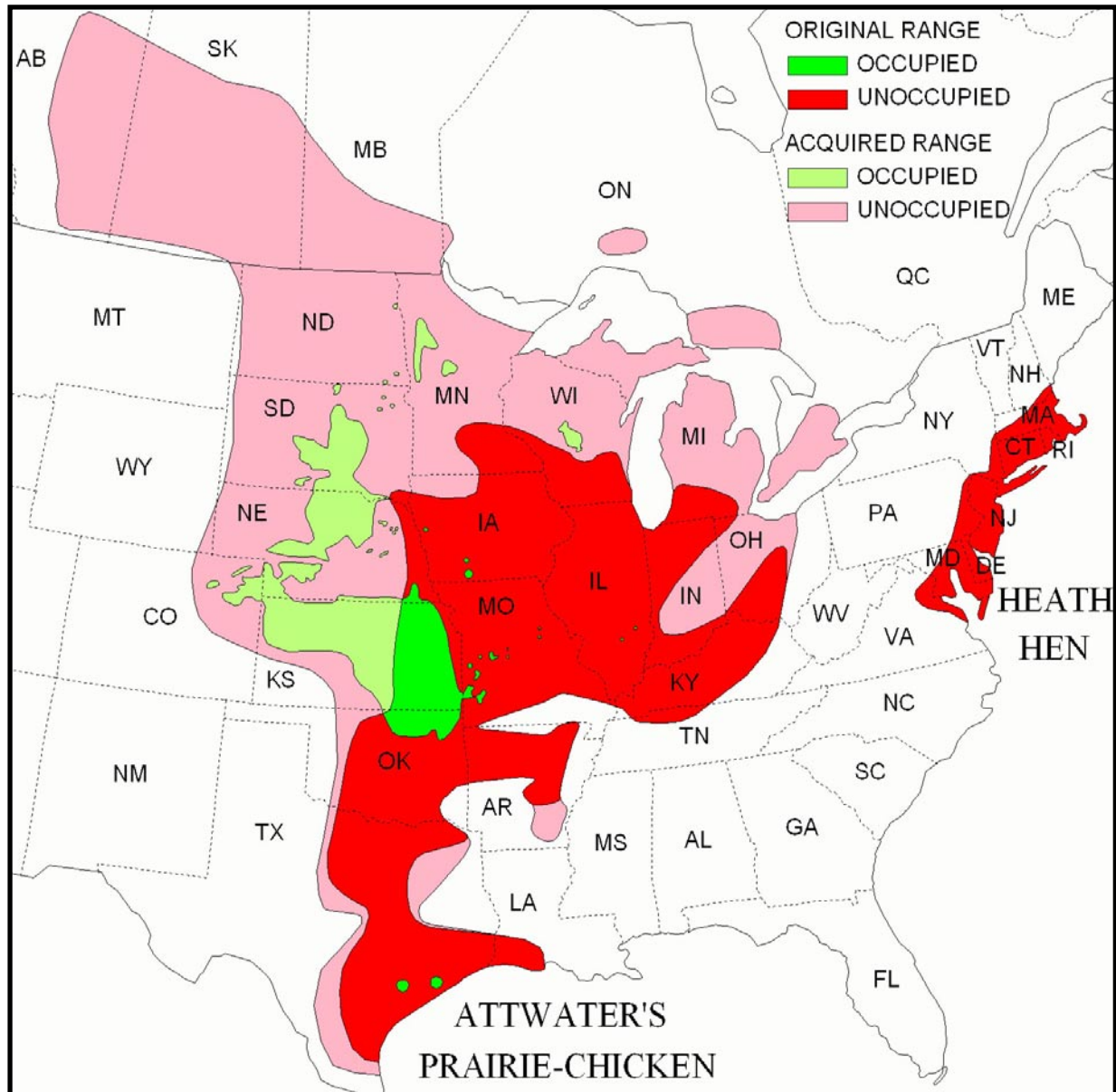


Figure 2. Original (pre-European settlement), acquired, and current distribution of greater prairie-chickens in North America.

“...essential in diagnosing the behavior of populations, and in appraising the opportunities for management.” (Leopold 1931:163). Range expansion of greater prairie-chickens to the north and west during the 1800s shifted the distribution into suitable grasslands as far north as central Alberta, and westward to northeastern Colorado (**Figure 2**). It is estimated that greater prairie-chicken distribution moved northward at a rate of 10 km per year in Minnesota (Svedarsky et al. 1999) and westward approximately 25 km per year in Colorado (Van Sant and Braun 1990, Svedarsky et al. 1999). Similarly, greater prairie-chickens were uncommon in Kansas during the early 1800s, but by 1870 they

had reached Fort Hays and by 1897 were reported in Colorado (Applegate and Horak 1999, Giesen and Schroeder 1999). The change in geographic distribution is believed to have been facilitated by the expansion of settlement and agriculture practices and/or the ‘improvement’ of grasslands as bison (*Bison bison*) were eliminated from the prairies (Bergerud 1988a, Svedarsky et al. 2000). It is generally believed that the small farming operations of the 1800s created a mosaic of small grain fields interspersed with grasslands that protected favorable nest/brood habitat and provided a reliable source of winter food. While the change in the original distribution reflects the movement of pioneers

and settlement westward, it also highlights the ability of greater prairie-chickens to successfully use a variety of climate, soil, and vegetation conditions (Svedarsky et al. 2000).

Peak populations of greater prairie-chickens occurred at different times for the various states throughout their geographic distribution; in many cases populations were increasing in the western portions of the range concurrent with declines in eastern portions (Schroeder and Robb 1993). Although precise estimates of historical abundance are difficult to determine "...in the late 1800's and early 1900's greater prairie-chicken numbers were so tremendous in a vast area of the Great Plains that they more or less created a 'chicken hunting culture'..."; however, "...this era of 'super abundance' eventually ended as habitat loss, habitat succession, excessive market kills, weather, and other factors led to declining populations in many states" (Hier 1999:162).

Greater prairie-chickens are currently distributed in remnant tallgrass prairie in the eastern portions of

their range, and in mixed, mid-tallgrass prairies in the western portions (**Figure 2**; Aldrich and Duvall 1955, Aldrich 1963, Svedarsky et al. 2000). The core of their distribution has shifted west by approximately 800 km since pre-settlement times, and greater prairie-chickens are now most abundant and widely distributed in portions of their acquired range (**Figure 2**). Data from Breeding Bird Surveys (**Figure 3**) and Audubon Christmas Bird Counts (**Figure 4**) show a similar distribution, but they are not as precise because of the infrequent observations of greater prairie-chickens and the small number of regular surveys. Greater prairie-chicken range is most extensive in Nebraska and Kansas with smaller populations in South Dakota, Colorado, Oklahoma, Minnesota, and Wisconsin. Relatively small and isolated populations occur in North Dakota, Missouri, Illinois, and Iowa.

Population estimates of greater prairie-chickens are usually based on counts of males at display grounds (leks) and/or harvest data. Although lek count and harvest data show considerable annual

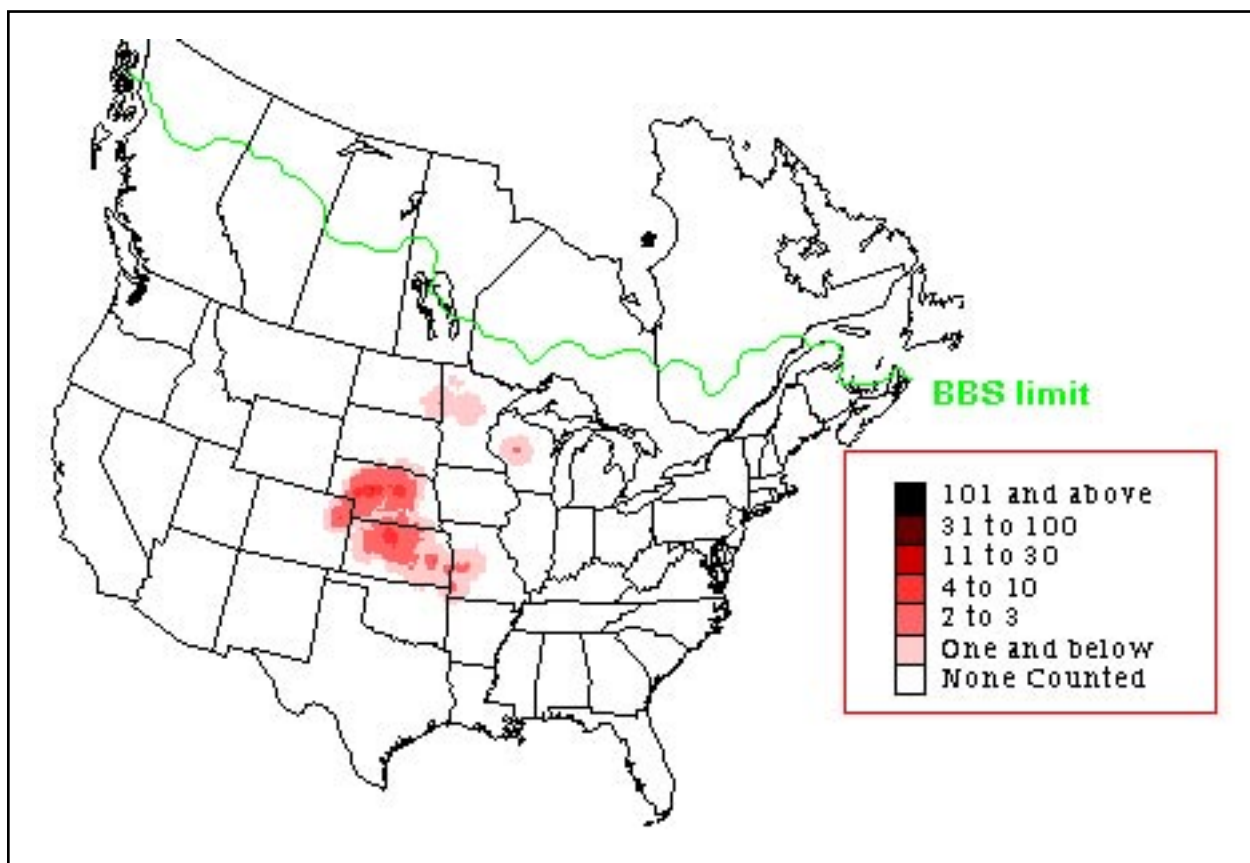


Figure 3. Distribution of greater prairie-chickens in North America as estimated with U.S. Fish and Wildlife Service Breeding Bird Surveys (BBS) (<http://www.mbr-pwrc.usgs.gov/bbs/grass/h3050ra.htm>, December 1, 2004). The different colors refer to the likely number of observations on a given breeding bird survey.

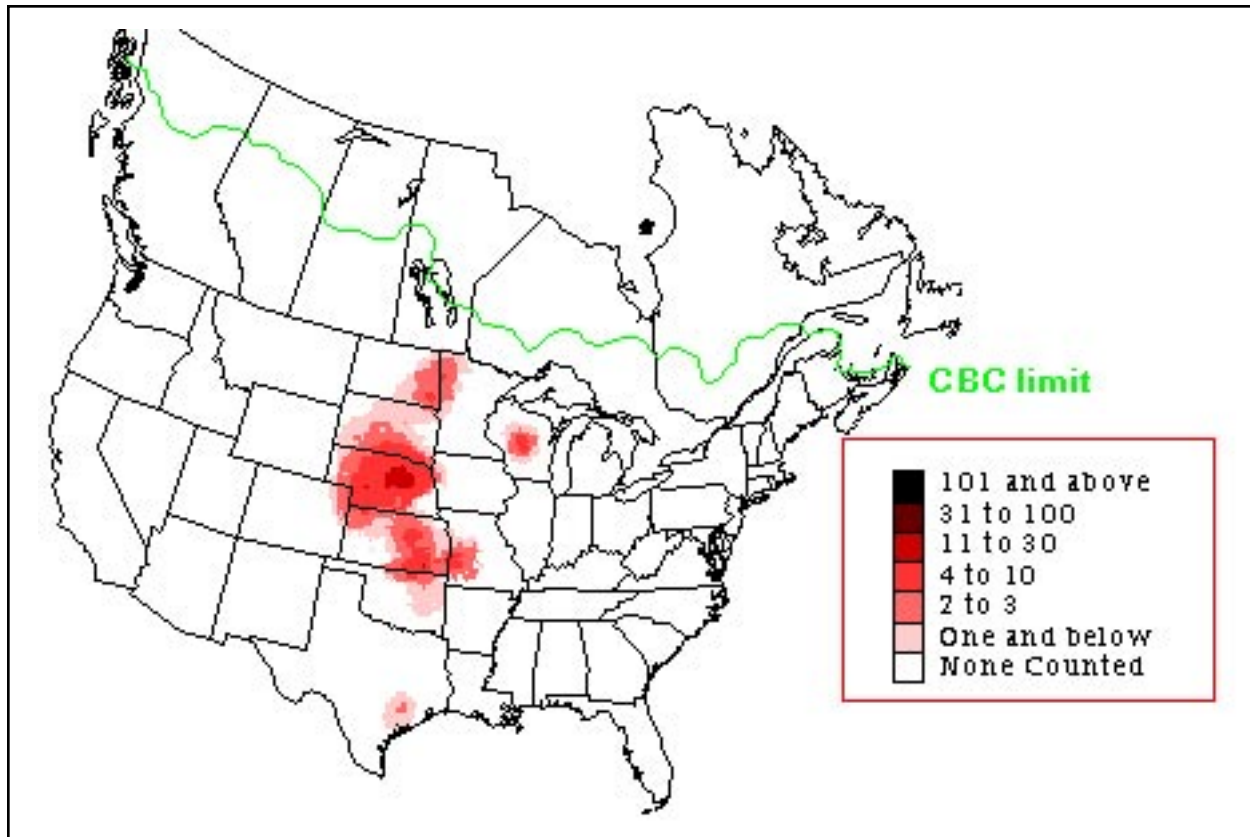


Figure 4. Distribution of greater prairie-chickens in North America as estimated with the Audubon Society's Christmas Bird Counts (CBC) (<http://www.mbr-pwrc.usgs.gov/bbs/grass/c3050ra.htm>, December 1, 2004). The different colors refer to the likely number of observations for a given Christmas bird count.

and regional variation, when examined over the long term (in some cases several decades) they provide useful information regarding long-term population trends (see Connelly et al. 2004 for example with greater sage-grouse). Recent range-wide population estimates, compiled by Svedarsky et al. (2000), indicate that greater prairie-chickens have generally declined throughout their geographic distribution during the past 30 years. Exceptions to this trend are Colorado, where populations have increased, and Wisconsin and Nebraska where populations have remained somewhat stable. Declines have been precipitous in Oklahoma, which had an estimated 130,000 greater prairie-chickens in 1968 and 1,500 birds in 1997, and in Kansas, which had an estimated population of 530,000 greater prairie-chickens in 1989 and 160,000 by 1997. Current range-wide estimates of the population vary between 370,000 and 690,000 birds distributed in 11 states (Storch 2000, Svedarsky et al. 2000, Rich et al. 2004). The core of the greater prairie-chicken population is found in parts of Kansas, Nebraska, and South Dakota, while smaller more isolated populations are found in other states (Svedarsky et al. 2000).

The capacity of various grassland habitats to support greater prairie-chickens may vary throughout the North American range. For example, although localized density estimates for males may be as high as 8.1 to 36.0 males per km² (Hamerstrom et al. 1957, Westemeier and Gough 1999, Westemeier et al. 1999), typical density estimates range between 0.3 to 2.5 males per km² (Kobriger et al. 1988, Anderson and Toepfer 1999, Fredrickson et al. 1999).

Historical and current regional distribution and abundance in South Dakota

In a recent review of the grouse species observed by Meriwether Lewis and William Clark during their 1803 – 1806 expedition, Zwicker and Schroeder (2003) suggest that greater prairie-chickens were common from the confluence of the Mississippi and Ohio rivers to the confluence of the James and Missouri rivers (present day Nebraska/South Dakota border). Although Fredrickson et al. (1999) cite an 1804 diary entry by Clark, who noted “prairie hens” near the Big Bend area of South Dakota, as evidence that greater

prairie-chickens were common in the Dakotas prior to settlement, it is more likely that these birds were sharp-tailed grouse, as argued by Zwickel and Schroeder (2003). Exactly when greater prairie-chickens expanded their range in central South Dakota is not clear, but by 1888 they were found across two thirds of the state as far west as Corson and Bennett counties (Fredrickson et al. 1999). Historical accounts of harvest information suggest that greater prairie-chickens were abundant at this time (Hier 1999). Populations declined however, due to habitat conversion, and by the 1920s were absent from much of the eastern part of the state.

A statewide population estimate in 1968 was approximately 80,000 greater prairie-chickens. By 1982 the statewide estimate had declined to 39,000 greater prairie-chickens distributed on 23,750 km², predominately in the south-central part of the state. Greater prairie-chickens again expanded their distribution to the east and north when a considerable portion of the state was enrolled in the Conservation Reserve Program (CRP) during the mid-1980s (Fredrickson et al. 1999). The CRP is a federal program initiated in the mid-1980s to conserve water, soil, and wildlife resources by paying farmers to plant and maintain perennial cover crops of grasses, forbs, and shrubs. Increased precipitation levels in some years are believed to have had a positive effect on range conditions, and indirectly on greater prairie-chickens, by promoting growth of herbaceous cover required for nesting and brood rearing. The Fort Pierre National Grassland is a key area for greater prairie-chickens in the state, and populations there have reportedly increased in recent years coincident with a reduction in grazing pressure and implementation of rest-rotation grazing practices (Svedarsky et al. 2000). Populations in South Dakota are projected to fluctuate, with increases in some areas and declines in others (Westemeier and Gough 1999). The statewide estimate of abundance for 1997 was 65,000 greater prairie-chickens primarily located in the central and south-central area of the state, especially Stanley, Jones, Lyman, Buffalo, and Gregory counties (Fredrickson et al. 1999, Westemeier and Gough 1999).

Historical and current regional distribution and abundance in Nebraska

Although Lewis and Clark apparently observed greater prairie-chickens as they traveled north on the Missouri River during late summer in 1804 (along what is now the Nebraska/Iowa border; Zwickel and Schroeder 2003), there is little historical evidence of greater prairie-chickens elsewhere in Nebraska

prior to 1850 (Vodehnal 1999). However, greater prairie-chickens were sold in Omaha and Nebraska City during 1854, and by the late 1860s, when the initial surge of homesteaders moved west, populations inhabited all of the eastern and southern parts of the state (Vodehnal 1999). Evidence suggests that a peak in greater prairie-chicken abundance occurred during the 1860s and 1870s. In 1874 alone, market hunters shipped at least 300,000 greater prairie-chickens out of 19 counties in Nebraska to cities in the east (Vodehnal 1999). Greater prairie-chickens moved into the Sandhills (primarily Sheridan, Cherry, Grant, Hooker, Thomas, Arthur, McPherson, Keith, Lincoln, Custer, Logan, Garden, Garfield, Brown, Rock, Blaine, Loup, Holt, and Wheeler counties) during the early 1900s when settlers were allowed to claim and farm acreage in this region; populations eventually declined in the early 1920s as cultivation became more extensive. A combination of habitat loss due to cultivation of native grasslands, and habitat degradation due to changes in grazing of ranges during the drought of the Dust Bowl, is believed to have nearly extirpated greater prairie-chickens from the state during the late 1930s (Vodehnal 1999). However, introduction of improved range management practices (such as deferred grazing) restored habitat for greater prairie-chickens and populations subsequently rebounded.

Although greater prairie-chickens may at one time have inhabited all of Nebraska, they are currently restricted to the Sandhills (especially the eastern and southern edges), counties in the extreme southeast, and parts of the southern border with Kansas. The heart of the population is concentrated in Holt, Rock, Garfield, and Wheeler counties (Vodehnal 1999). Localized populations outside the Sandhills are thought to create a broader distribution that connects South Dakota, northeastern Colorado, and northern Kansas (Westemeier and Gough 1999).

Recent population estimates for Nebraska have focused on the Sandhills (Vodehnal 1999). Although greater prairie-chickens are found outside this region, the habitat tends to be fragmented and the populations localized. Center-pivot irrigation was introduced to the Sandhills in the 1960s and resulted in conversion of substantial grassland to cropland. Population estimates suggest that about 100,000 greater prairie-chickens were present in Nebraska during 1968. By 1978 approximately 216,515 ha of grassland habitat had been converted, 85 percent of which occurred in the nine counties comprising the heart of the greater prairie-chicken distribution (Vodehnal 1999). Numbers increased to approximately 200,000 birds by 1979

and remained there until declining to 130,000 greater prairie-chickens by 1997 (Svedarsky et al. 2000). Increases in populations in the Sandhills during the late 1980s are believed to have occurred in response to cultivated lands being enrolled in the CRP (Vodehnal 1999). Populations in Nebraska are generally believed to be 'secure' (Svedarsky et al. 2000). The estimate of greater prairie-chicken abundance for 1996 places the Nebraska population (estimate for Sandhills only) at about 130,000 (Vodehnal 1999). However, since most greater prairie-chickens occur on private lands, populations are affected by changes in land use practices and the economics of livestock production. Distribution of greater prairie-chickens outside the Sandhills is restricted by a higher ratio of cropland to grassland; habitat in the southwestern part of the state is 45 to 75 percent rangeland and 30 to 50 percent cropland, and habitat along the southern edge is 37 to 43 percent rangeland and 53 to 60 percent cropland (Vodehnal 1999).

Historical and current regional distribution and abundance in Colorado

Greater prairie-chickens are believed to have been absent from Colorado prior to settlement and the introduction of row crops (Giesen and Schroeder 1999). The first recorded observation of greater prairie-chickens was in 1897 in the northeastern part of the state near Julesburg, Sedgewick County. As cultivation of small grains increased, greater prairie-chickens expanded their range westward across the state. In 1907 a nest was located near Barr Lake, Adams County, approximately 250 km straight line distance from where greater prairie-chickens were initially reported in 1897; this record is the furthest west greater prairie-chickens were ever observed in Colorado. The maximum distribution of greater prairie-chickens in Colorado occurred from 1897 to the mid-1930s and included as many as 9 to 11 counties in the northeastern corner of the state (Van Sant and Braun 1990, Giesen and Schroeder 1999).

It is not clear when greater prairie-chickens were most abundant in Colorado as early records are uncommon. However, there is evidence that numbers may have begun to decline by the mid-1930s in response to factors such as drought, heavy grazing, market hunting, and loss of habitat as extensive cultivation replaced the usual practice of 'patchwork' farming (Evans and Gilbert 1969, Pusateri 1990, Van Sant and Braun 1990, Giesen and Schroeder 1999). Approximately 2,800 greater prairie-chickens are believed to have been present in Colorado during the 1950s, but the population had declined to an estimated

600 to 700 by 1963 (Van Sant and Braun 1990, Giesen and Schroeder 1999). In 1973 the greater prairie-chicken was listed by the Colorado Wildlife Commission as endangered in Colorado based on a total population estimate of 600 birds in Yuma, Washington, and Logan counties (Giesen and Schroeder 1999).

Restoration of some grain fields under the CRP during the mid-1980s, seeding with warm season grasses, and prescribed burning are believed to have had positive impacts on greater prairie-chicken distribution and range in Colorado during the past 20 years (Giesen and Schroeder 1999). Increased levels of annual precipitation between 1989 and 1998 may have also had a positive impact by promoting vegetation growth, resulting in better range conditions and cover for greater prairie-chickens (Westemeier and Gough 1999). This species' range also expanded during the 1990s as a result of translocations. Current populations are estimated at 8,000 to 10,000 greater prairie-chickens. The species is not currently listed (Svedarsky et al. 2000). The core of the population is located on private land in Phillips, Yuma, and Washington counties, with most birds in Yuma County (Giesen and Schroeder 1999). Three introduced populations occur in the following areas: one near the intersection of Logan, Sedgewick, and Washington counties; one in Morgan and Washington counties; and one in Weld and Morgan counties. Populations of the introduced greater prairie-chickens are estimated to total 300 to 400 birds (Giesen and Schroeder 1999).

Historical and current regional distribution and abundance in Kansas

Pre-settlement records of greater prairie-chickens in Kansas are rare and often ambiguous. However, evidence suggests that greater prairie-chickens expanded westward during the 1860s and 1870s as agriculture and settlement moved across the state (Applegate and Horak 1999). Greater prairie-chickens were first reported near Fort Hays around 1870, and in northwestern Kansas by the late 1890s. Abundance of greater prairie-chickens is believed to have peaked in Kansas during the late 1870s and 1880s (Applegate and Horak 1999, Svedarsky et al. 2000). The quantity of occupied range appeared to be declining by 1891, and consequently, hunting seasons were temporarily closed in many counties; despite these efforts populations continued to decline (Applegate and Horak 1999). By 1912, declines in eastern Kansas were clear, and by the 1930s declines were apparent in northwestern Kansas. As a result of drought conditions, and the associated heavy grazing of rangelands, populations also were

nearly eliminated from parts of eastern Kansas during the 1930s (Applegate and Horak 1999).

Although much grassland habitat in eastern Kansas was converted to cropland, the tallgrass prairies in the Flint Hills were largely preserved, as shallow soils in the region precluded extensive cultivation (Applegate and Horak 1999). Consequently, the Flint Hills area (primarily Clay, Riley, Pottawatomie, Dickinson, Geary, Wabaunsee, Morris, Marion, Chase, Butler, and Cowley counties) has traditionally been the prime greater prairie-chicken range in Kansas. The estimated population was 450,000 in 1968, 880,000 in 1979, 540,000 in 1985, 530,000 in 1989, and 160,000 in 1997 (Applegate and Horak 1999, Svedarsky et al. 2000). Population estimates indicate that as much as 44 percent of the greater prairie-chicken population in Region 2 may be found in Kansas, thus major population declines in this state may impact long-term viability of greater prairie-chickens throughout their range.

The current practices of early intensive grazing, coupled with annual burning of large grassland pastures, may be detrimental to greater prairie-chicken nesting and brood-rearing habitat, especially in the traditional greater prairie-chicken stronghold of the Flint Hills (Applegate and Horak 1999). Declines in greater prairie-chicken numbers suggest that current land management practices are adversely affecting populations in Kansas (Svedarsky et al. 2000). Future population trends are expected to show a decline given that few areas in the state are managed specifically for greater prairie-chickens (Westemeier and Gough 1999).

Discontinuities in regional distribution

Several sources of information can be used to evaluate discontinuities in the distribution of greater prairie-chickens. First, research on their behavior in relatively continuous habitat has indicated that dispersal/migration distances may be greater than 10 km (Schroeder and Braun 1993, Svedarsky and Van Amburg 1996). Second, behavioral and genetic research in discontinuous habitat has provided some basic information on the quantity of unsuitable habitat necessary to prevent or restrict movement between adjacent populations (Westemeier et al. 1998, Bellinger et al., 2003, Johnson et al. 2003). For example, recent genetic analysis of greater prairie-chicken subpopulations in central Wisconsin indicates that separation of only 20 km between areas of occupied habitat may be enough to limit gene flow (Johnson et

al. 2003, 2004). Third, information on habitat use by greater prairie-chickens (Christisen 1969, Kirsch 1974, Svedarsky et al. 2000) and the distribution of suitable habitats throughout large portions of their range (see further discussion in Regional habitat section) may be used to evaluate where connecting habitats are limited and/or where populations are likely to be isolated.

There appear to be two large, relatively continuous distributions of greater prairie-chickens (**Figure 2**): one in South Dakota and Nebraska and the other in Nebraska, Colorado, Kansas, Oklahoma, and Missouri. All other populations appear to be relatively small and/or isolated; many of these have effective breeding populations of less than 500 individuals, which may not be adequate to prevent loss of genetic heterogeneity (Lande and Barrowclough 1987, Soulé 1987). The continuity of the two largest populations of greater prairie-chickens is likely over-estimated. This occurs, in part, because large populations tend to be sub-sampled (Vodehnal 1999) while small populations are completely counted (Westemeier et al. 1998, Silvy et al. 1999). Consequently, there is a tendency to estimate distributions of larger populations on a 'rougher scale' than those of smaller populations. Hence, it is possible that the larger populations may not be as continuous as they are represented. Improvements in the quality of distribution data may eventually highlight additional areas where population isolation is an issue.

Activity patterns and movements

Circadian

Greater prairie-chickens are most likely to feed during the morning and evening; they typically loaf during the day and roost at night (Schroeder and Robb 1993). They are easily observed during the spring courtship display when males and females visit leks for mating. Although radio-telemetry has made it possible to monitor greater prairie-chickens and to record their activities, detailed behavioral observations are difficult to obtain, as greater prairie-chickens typically flush more readily than species such as white-tailed ptarmigan (*Lagopus luecurus*). For instance, the flushing distance of a greater prairie-chicken in response to a human observer averaged 31 m but was as great as 119 m for greater prairie-chickens in Nebraska grasslands (Mohler 1952); white-tailed ptarmigan, on the other hand, can sometimes be caught by hand. Furthermore, grassland habitats with adequate cover (vertical and horizontal) generally restrict viewing opportunities for a species that spends most of its time on the ground.

Winter season

Flocks are often large and tend to become more established as winter progresses; sometimes as many as 100 to 200 greater prairie-chickens may be in a flock (Yeatter 1943, Hamerstrom and Hamerstrom 1949, Mohler 1963, Manske and Barker 1981, Toepfer and Eng 1988). Behavioral observations of winter flocks indicate that they often break into smaller groups, especially early in the winter season. However, as weather conditions become severe, flocks tend to become less mobile and more stable (Hamerstrom and Hamerstrom 1949, Baker 1953).

Toepfer and Eng (1988) monitored daily activity patterns of radio-marked individuals throughout the winter in North Dakota and determined a general pattern of flock behavior. At sunrise, birds would fly 0.8 to 1.6 km from night roost sites to feeding areas (in this study, agriculture fields). Similar patterns of behavior were noted for winter flocks observed by Hamerstrom and Hamerstrom (1949) in Wisconsin, Horak (1985) in Kansas, and Mohler (1952) in Nebraska. Mohler (1952) noted that feeding periods lasted an average of 82 minutes but ranged anywhere from 45 to 150 minutes depending on weather conditions and disturbance of the flock by potential predators. Following the morning feeding period, birds flew or walked to a site where they loafed (Toepfer and Eng 1988). During late afternoon, flocks again returned to feeding areas before flying to night roost sites. Although flocks generally use the same daily feeding areas, they typically roost in different locations on consecutive nights. Flocks often use the same feeding areas for extended periods during winter (Hamerstrom and Hamerstrom 1949, Mohler 1952), but they will move to different areas in response to changes in snow depth (Toepfer and Eng 1988).

Greater prairie-chickens mitigate conditions of cold and wind during the winter by sitting in snow depressions and snow burrows (Toepfer and Eng 1988). During extreme conditions of snow and/or cold, greater prairie-chickens may remain longer at roost sites, up to 17 hours, and occasionally may roost the entire day (Hamerstrom and Hamerstrom 1949, Toepfer and Eng 1988). Average distance between neighboring individuals at a winter roost site was 3.3 m ($n = 261$) in North Dakota (Toepfer and Eng 1988).

Caution should be exercised when comparing estimates of home range size due to differences in methodologies, assumptions, and biases of the various studies; for example, convex polygons (Toepfer and

Eng 1988) and 75 percent probability contour generated with harmonic means (Schroeder and Braun 1992a) may not be directly comparable. Winter home range size for birds averaged 8.4 km² on the Sheyenne National Grassland in North Dakota ($n = 14$; Toepfer and Eng 1988), was approximately 2.6 km² in Kansas (Horak 1985), and 3.4 km² in Colorado ($n = 35$; Schroeder and Braun 1992a). Hamerstrom and Hamerstrom (1949) recorded a daily movement radius of 0.8 to 1.6 km for flocks in Wisconsin. In North Dakota, flocks tended to remain within 3 km of a known lek site, and males spent the winter an average distance of 2.8 km ($n = 4$) from their home lek while females were an average of 4.3 km away ($n = 12$; Toepfer and Eng 1988). Similar findings were recorded in Wisconsin where a high proportion of males (94 percent) remained within 4.8 km of their home lek during winter (Hamerstrom and Hamerstrom 1973).

Spring season

Most spring activity is focused near lek sites. Based on 8,000 observations of radio-marked greater prairie-chickens and 22,000 observations of non-radioed birds in central Wisconsin, 92 percent of all locations were within 2 km of a lek (Toepfer 1988). During early spring, males begin to visit leks while females tend to localize near their eventual nest site (Hamerstrom and Hamerstrom 1949, Toepfer and Eng 1988, Schroeder and Braun 1993). Toepfer and Eng (1988) noted that females remained relatively sedentary for the first four weeks following snow melt, moving on average 0.6 km between feeding and roosting areas. Males had greater mobility at this time, attributed to movements between lek sites and feeding areas. A decrease in daily movements of males between late winter and spring was found to coincide with an increased use of grassland near the lek for feeding, loafing, and roosting (Drobney and Sparrowe 1977). Additionally, males spent a greater proportion of their time on leks during April and May.

Average home range size for greater prairie-chickens in Colorado varied among age classes and sexes during spring: adult males 168 ha, yearling males 642 ha, adult females 320 ha, and yearling females 450 ha (Schroeder and Braun 1992a). In Kansas, yearling males also had larger home ranges than adult males, 186 ha and 108 ha respectively (Bowman and Robel 1977). The large home range size of yearling males may result from their attempts to establish breeding territories on leks (Bowman and Robel 1977, Schroeder and Braun 1992b). Home range sizes of females monitored in Minnesota decreased from 82 ha in early spring to 31 ha

in late spring, reflecting changes in female reproductive behavior; by late spring females had commenced laying and incubating (Svedarsky 1988).

Females may initiate laying 1 to 5 days after copulation and usually lay one egg per day with occasional skips of 1 to 3 days (Lehmann 1941, Svedarsky 1988). Nest visits to lay eggs usually occur between 0800 and 1400 hours (Svedarsky 1988). When females commence incubation, daily movements decrease and are restricted to feeding forays, usually 0.4 to 1.6 km from the nest site, during the morning and afternoon (Gross 1930, Lehmann 1941, Svedarsky 1988). The early morning incubation recess may be skipped late in incubation (Lehmann 1941). Females incubate their clutches for 23 to 25 days (Schroeder and Robb 1993). Females are able to initiate a second, and sometimes a third, clutch following predation, abandonment, and/or destruction of their first nest. The probability of a female reneesting is related to the timing of nest loss; females are able to renest if their first clutch is lost during laying or early - mid incubation, but not late in incubation (Svedarsky 1988). Females return to a lek to mate prior to commencing a renest unless the nest is lost during egg laying, in which case they will lay eggs in a new nest without mating again. Hamerstrom and Hamerstrom (1973) noted a bimodal distribution of copulations on leks and concluded that females visiting the lek to mate during late spring were most likely reneesting birds.

Summer season

During the summer, greater prairie-chickens tend to forage in the cooler part of the day and rest in shade during mid-day. Birds often take dust baths in dry, powdery soil (Lehmann 1941, Yeatter 1943). In general, home range size for greater prairie-chickens tends to be smaller during summer when the birds are molting. Males often remain close to their lek site and may frequently visit the lek even though there is no breeding activity (Hamerstrom and Hamerstrom 1949). In North Dakota, females with broods may use relatively small areas, on average 14 ha, within their total range for as long as 7 to 57 days (Newell et al. 1988). Broods are most active, feeding and traveling, during the cooler part of the day; loafing, resting, and dust bathing are common during the heat of mid-day (Horak 1985). Broods may combine in late summer, and it is not uncommon to observe a group of different-aged chicks accompanied by two or more females (Yeatter 1943). Flocks of 25 to 50 juvenile birds have been observed in Kansas as early as August (Horak 1985).

Autumn season

Break-up of greater prairie-chicken broods commences in late summer but is most common in autumn (Lehmann 1941, Bowman and Robel 1977). In general, brood break-up is a gradual process with individuals leaving at different times (Bowman and Robel 1977). Daily movements of juveniles may be greater than those for adults during late autumn in Kansas; juveniles averaged 0.8 km per day while adult birds moved on average 0.6 km per day (Bowman and Robel 1977). Greater mobility of juvenile greater prairie-chickens may reflect their attempts to join a flock. Flock size tends to increase as autumn progresses, and by late autumn flocks may number from 30 to 150 birds (Yeatter 1943, Hamerstrom and Hamerstrom 1949). Early season flocks are unstable and commonly form only during feeding periods (Hamerstrom and Hamerstrom 1949).

Broad-scale movement patterns

Like other species of prairie grouse, greater prairie-chickens spend most of their time on the ground but commonly fly when disturbed, and between foraging, breeding, loafing/roosting areas, and water sources (Schroeder and Robb 1993). Historical evidence suggests that greater prairie-chickens were "...more or less..." migratory between breeding and wintering areas (Leopold 1931:173). Leopold (1931) reviewed written and anecdotal accounts from the late 1800s and noted that large flocks of birds were known to move southward into areas of Illinois, Missouri, and Iowa during winter, supposedly as a result of winter conditions further north. He concluded that "...evidence points toward a former maximum annual mobility of several hundred miles in greater prairie-chickens, and to seasonal shifts of scores of miles." Biases in sex ratios at banding stations in Wisconsin were considered by Schmidt (1936) as evidence of migratory tendencies in greater prairie-chickens. He concluded that males wintered close to their lek sites while females moved into southern Wisconsin. The greater prairie-chickens Schmidt (1936) banded in the northern half of Wisconsin during winter were mostly males (88 percent; $n = 137$) while those in the southern half were mostly females (85 percent; $n = 321$). Gross (1930) also mentions that migrating greater prairie-chickens are predominately female birds. By the time of Leopold's review (1931), there were few, if any, first hand observations of large-scale migrations in greater prairie-chickens. Leopold (1931) attributed this lack of migration to decreased food competition due to reduced populations and increased food resources in the form of agricultural crops, especially corn.

Greater prairie-chickens are capable of, and do make, relatively long distance movements between wintering and breeding areas. In western Minnesota, they have been recorded moving up to 48 km (Svedarsky and Van Amburg 1996). Hamerstrom and Hamerstrom (1949) in Wisconsin had one band recovery 170 km from its banding location. Fredrickson et al. (1999) in South Dakota had one greater prairie-chicken move 43 km. Schroeder and Braun (1993) observed similar movements and referred to the birds in eastern Colorado as 'partial migrants'. They recorded some individuals moving up to 40 km between wintering and breeding areas while others moved less than 5 km. The ability of greater prairie-chickens to traverse relatively long distances in a short time has been observed by Toepfer et al. (1990) for greater prairie-chickens recently translocated. In one particular case, they recorded a female moving 64 km in three days; they also observed some females traveling 10 km per day for several consecutive days. Movements by females to their breeding areas tend to be direct and are usually completed in one to three days (Toepfer et al. 1990).

In northeastern Colorado, females tended to migrate later than males during spring (late March versus late February) and moved significantly greater and more variable distances (mean = 9.2 km, range = 0.6 – 40.0 for females vs. mean = 2.7 km, range = 1.0 – 6.1 km for males; Schroeder and Braun 1993). These findings differ somewhat from Toepfer and Eng (1988) who reported a mean maximum distance of 6.3 km for females and 3.3 km for males between wintering and breeding areas on the Shewen National Grassland in North Dakota. Most of the long-distance movements recorded by Schroeder and Braun (1993) were completed by females; 35 percent of females (21 of 60) moved more than 5 km vs. 4.5 percent of males (1 of 22). Although the timing of female movement from wintering to breeding areas occurred relatively synchronously during late March in eastern Colorado, the return movement, from breeding to wintering areas, was extremely variable and reflected a female's brood status (Schroeder and Braun 1993). Unsuccessful females moved back to their wintering areas in early and mid-June ($n = 23$) while the date of migration for females with broods was early August to mid-September ($n = 10$).

Explanations of seasonal movement patterns observed for greater prairie-chickens are varied and may not be mutually exclusive. Schroeder and Braun (1993) suggested that greater prairie-chicken dispersal tendencies and philopatry to their first wintering and breeding areas were factors contributing to the pattern of movements they observed in eastern Colorado. Birds

in their study returned to within 1 km of the winter area used the previous year, despite moving more than 20 km to breeding areas. Additionally, females tended to establish nest sites within 0.8 km of those established the previous year. Regional variation in food availability (Gross 1930, Hamerstrom and Hamerstrom 1949, Toepfer and Eng 1988) and weather (Hamerstrom and Hamerstrom 1949) have also been suggested to play a role in migration. However, Svedarsky and Van Amburg (1996) suggest that although birds move to sources of winter food, as observed by shifts in winter flock locations, winter food resources may not be as limiting as people assume. During a particularly harsh winter in western Minnesota, they noted that two greater prairie-chickens moved 10 to 13 km; during the previous winter 10 individuals moved 16 to 24 km. Similarly, birds monitored by Schroeder and Braun (1993) routinely migrated to areas that other birds had vacated and *vice versa* in a region where food (corn) was available year-round. Moreover, they recorded considerable migration between breeding and wintering areas during mid-summer, a time of relative food abundance and moderate temperatures.

Population connectivity

There are no obvious natural barriers impeding the connectivity of greater prairie-chicken populations throughout most of their range. However, habitat alteration (see further discussion in Regional habitat section) has clearly created large areas that are mostly uninhabitable by greater prairie-chickens. Many of these unoccupied areas appear large enough to prohibit, or to slow, the frequency of movements by greater prairie-chickens between patches of occupied habitat. Research on greater prairie-chickens in relatively small, isolated populations suggests that seasonal movements are smaller than they are in relatively inter-connected habitats (Toepfer and Eng 1988, Schroeder and Braun 1993). In addition, populations separated by 10 to 20 km of unsuitable habitat appear to have gene flow that is insufficient to maintain genetic heterogeneity (Bellinger et al. 2003; Johnson et al. 2003, 2004).

Habitat

Regional habitat

The greater prairie-chicken is a grassland species typically found in the mid-tallgrass and tallgrass regions of the Great Plains states (Christisen 1969, Robel et al. 1970b). In Region 2, greater prairie-chickens are generally found in areas of permanent grasslands where the topography is open and rolling with few

trees. The general vegetation types occupied by greater prairie-chickens include mixed-grass prairie (South Dakota), Sandhills prairie (Nebraska, Colorado), and tallgrass prairie (Kansas) (Evans 1968). These are the ecoregions defined as the Prairie Parkland, Great Plains Steppe Province, and Great Plains-Dry Steppe Province (<http://www.fs.fed.us/r2/nebraska/gpng/gpng.html>, December 1, 2004).

The Prairie Parkland Province of eastern South Dakota, Nebraska, and Kansas is characterized by gently rolling hills, forest-steppe vegetation, and Mollisols soils (<http://www.fs.fed.us/r2/nebraska/gpng/matrix/ecoregions.html>, December 1, 2004). The Great Plains Steppe Province of central South Dakota, Nebraska, and Kansas is characterized by flat and rolling plains and mixed-grass steppe vegetation. Soils are generally Mollisols; Entisol soils are found in the Sandhills of Nebraska. The Great Plains-Dry Steppe Province of western Nebraska, western Kansas, and northeastern Colorado, which is characterized by rolling plains and tablelands and shortgrass prairie, tends to have Mollisol soils with a high level of precipitated calcium carbonate (<http://www.fs.fed.us/r2/nebraska/gpng/matrix/ecoregions.html>, December 1, 2004).

The regional distribution of current habitats also can be illustrated for major portions of the greater prairie-chicken range in Region 2 using the physiographic areas as defined by the USGS for PIF. Although these physiographic areas were defined, in part, from data provided by Breeding Bird Surveys, they illustrate the distribution of major habitat types that are relevant to greater prairie-chickens. The seven relevant physiographic regions in Region 2 include Dissected Till Plains (**Figure 5**), Osage Plains (**Figure 6**), Central Mixed-grass Prairie (**Figure 7**), Northern Mixed-grass Prairie (**Figure 8**), Glaciated Missouri Plateau (**Figure 9**), Northern Tall Grass Prairie (**Figure 10**), and Central Short Grass Prairie (**Figure 11**). The quantities of general habitat categories are listed in **Table 1**.

Important habitat characteristics for greater prairie-chickens in all suitable vegetation types include: 1) large areas of open grassland with relatively dense residual cover for nesting, 2) suitable brood habitat adjacent to nesting habitat, 3) adequate cover for winter roost sites, and 4) interspersed cropland, especially in areas characterized by extensive winter snow cover (Svedarsky et al. 2000).

Habitat in South Dakota

Habitat in the core of the greater prairie-chicken's distribution in South Dakota (Fort Pierre National Grassland and Lower Brule Indian Reservation) is primarily mid-grass prairie on the Pierre-Promise-Risma-Soil Association. Average annual precipitation is 38 to 48 cm, and dominant grasses include western wheatgrass (*Agropyron smithii*) and green needlegrass (*Stipa viridula*) (Rice and Carter 1982).

Habitat in Nebraska

Greater prairie-chickens are currently found in three general areas of Nebraska: the Sandhills of central Nebraska, the grasslands in the extreme southwestern part of the state, and along the Kansas border where the Flint Hills extend into Nebraska (Vodehnal 1999). The core of the distribution lies in the Sandhills, which encompass approximately 50,000 km² in area, making it one of the largest stabilized sand dune regions in the world. Topography of the region is determined by prevailing winds that create large dunes that have a northwest-southeast orientation with higher, steeper slopes to the west and more rolling hills to the east (Robertson 1980, Vodehnal 1999). Dunes may be as high as 122 m and as long as 32 km, with slope angle up to 25 percent (Vodehnal 1999). The vegetation of this region is referred to as Sandhill Prairie and is unique to Nebraska (Robertson 1980). Dominant grass species on sandy upland sites include sand bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), prairie sandreed (*Calamovilfa longifolia*), switchgrass (*Panicum virgatum*), sand lovegrass (*Eragrostis trichodes*), blue grama (*Bouteloua gracilis*), and needle-and-thread (*Stipa comata*) (Vodehnal 1999). Average annual precipitation is 41 to 58 cm (Vodehnal 1999) with the higher precipitation levels occurring in the eastern part of the Sandhills (Robertson 1980). Average annual temperature is 9 °C, but the temperature can be as low as -40 °C and as high as 43 °C (Robertson 1980).

Habitat in Colorado

In northeastern Colorado, greater prairie-chickens were found to use habitats characterized by grass taller than expected, given its availability on the study area; cropland was used more than expected only during winter (Schroeder and Braun 1992a). Schroeder and Braun (1992a) cite the Sandhills habitat in Colorado

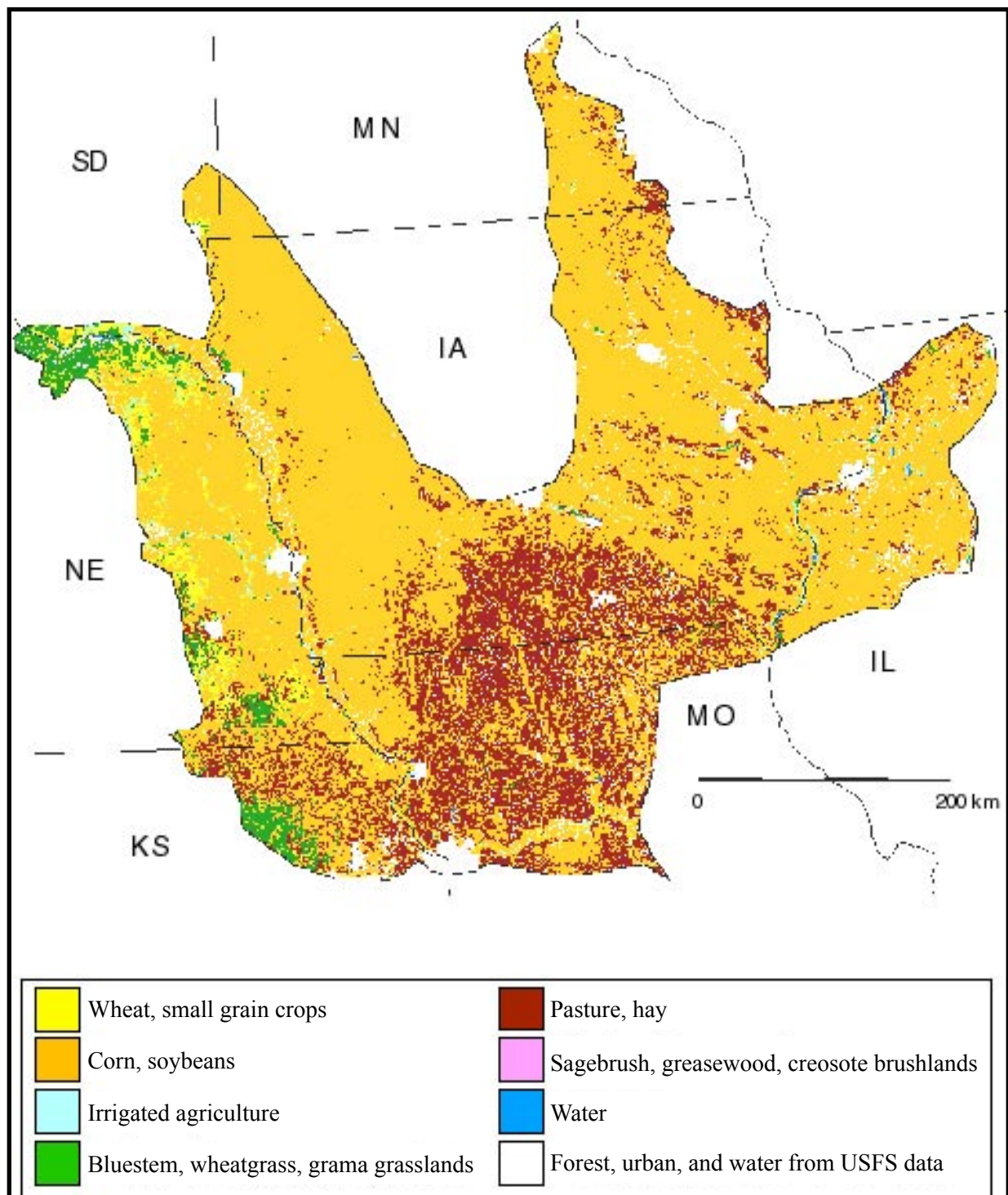


Figure 5. Distribution of major cover types in the 'Dissected Till Plains' physiographic area as estimated mostly with 1990 U.S. Geological Survey data and provided by Partners in Flight (<http://www.cast.uark.edu/pif/gif/32.nfor.gif>, December 1, 2004).

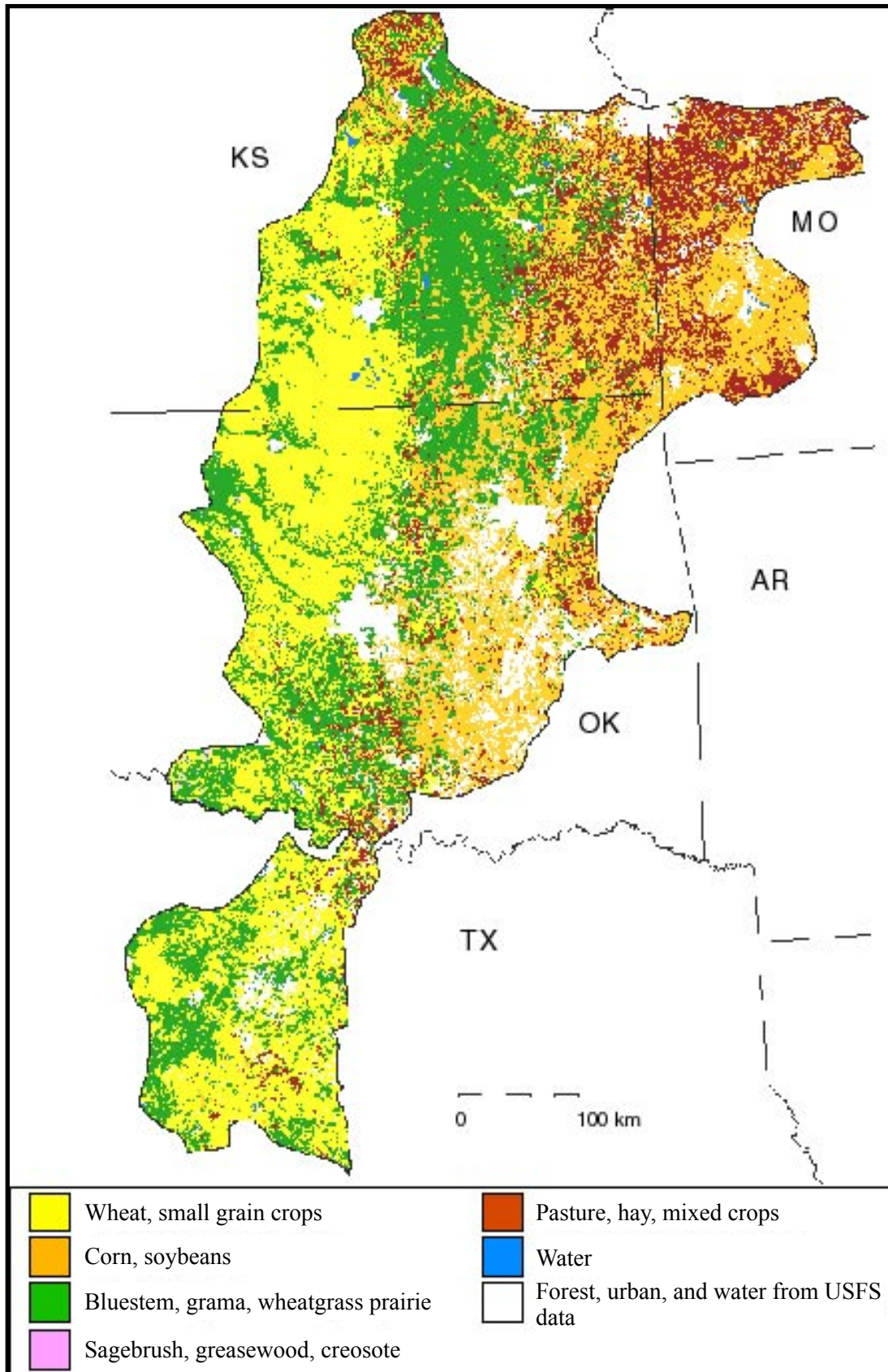


Figure 6. Distribution of major cover types in the 'Osage Plains' physiographic area as estimated mostly with 1990 U.S. Geological Survey data and provided by Partners in Flight (<http://www.cast.uark.edu/pif/gif/33.nfor.gif>, December 1, 2004).

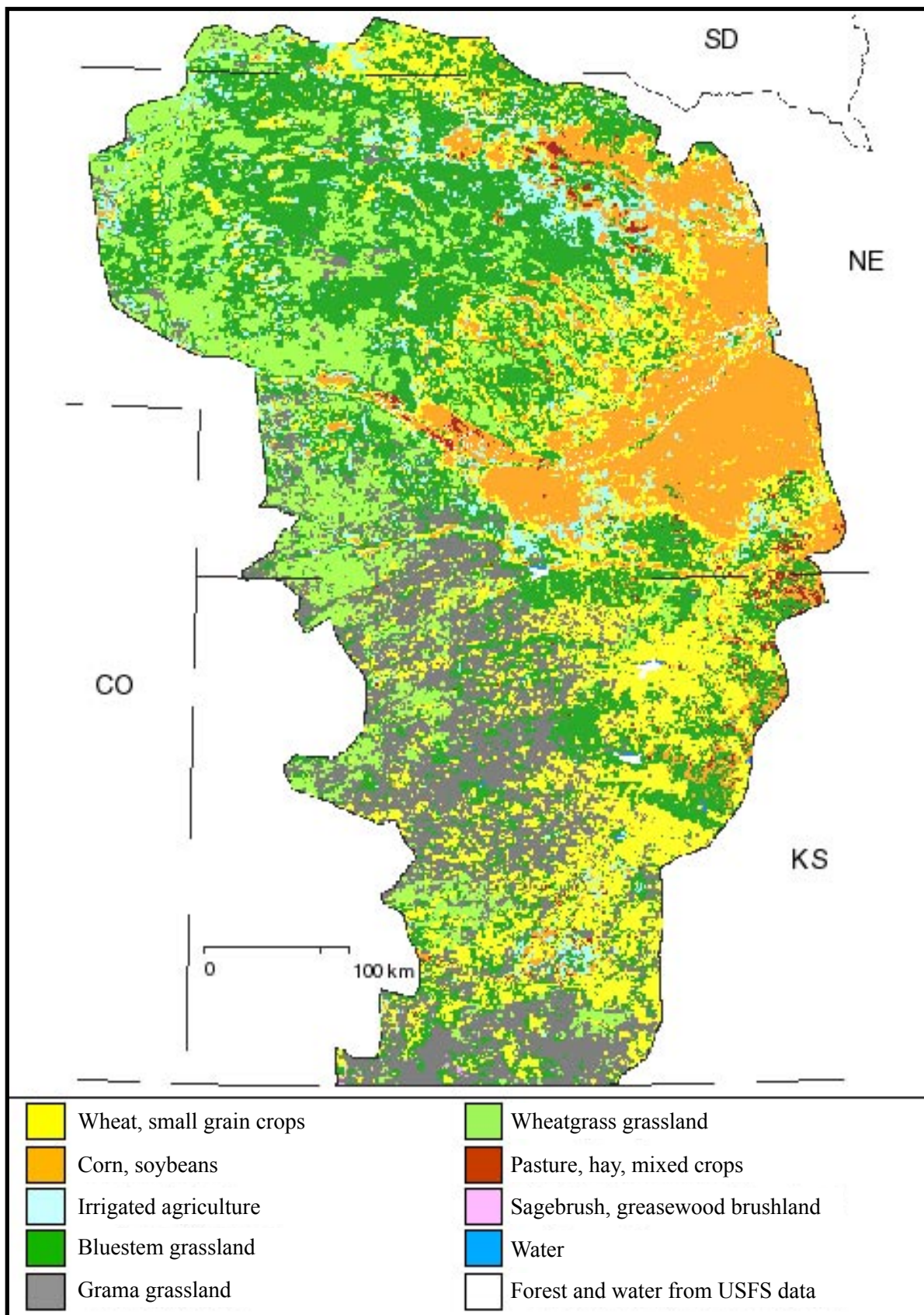


Figure 7. Distribution of major cover types in the ‘Central Mixed Grass Prairie’ physiographic area as estimated mostly with 1990 U.S. Geological Survey data and provided by Partners in Flight (<http://www.cast.uark.edu/pif/gif/34.nfor.gif>, December 2004).

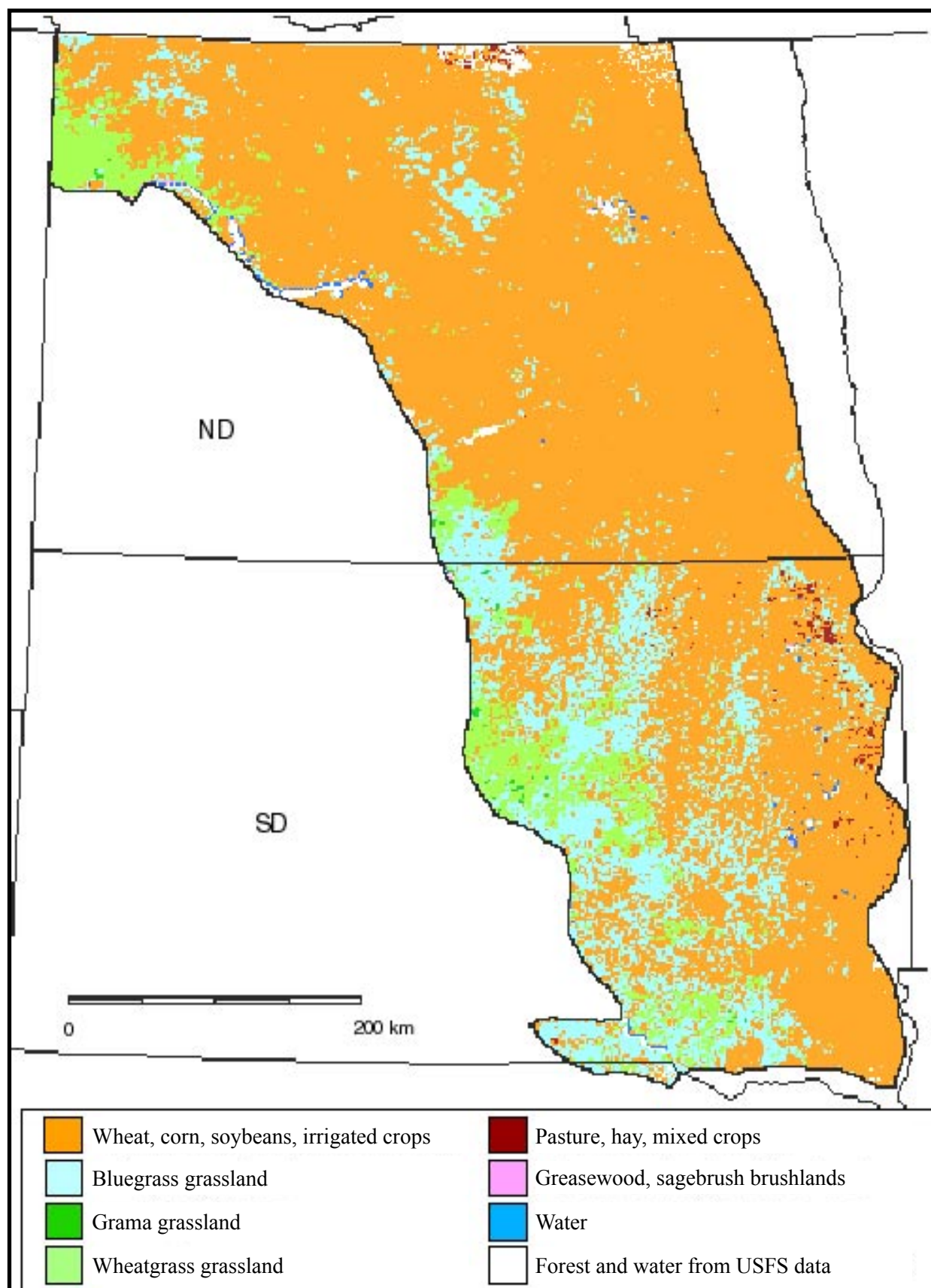


Figure 8. Distribution of major cover types in the 'Northern Mixed Grass Prairie' physiographic area as estimated mostly with 1990 U.S. Geological Survey data and provided by Partners in Flight (<http://www.cast.uark.edu/pif/gif/37.nfor.gif>, December 1, 2004).

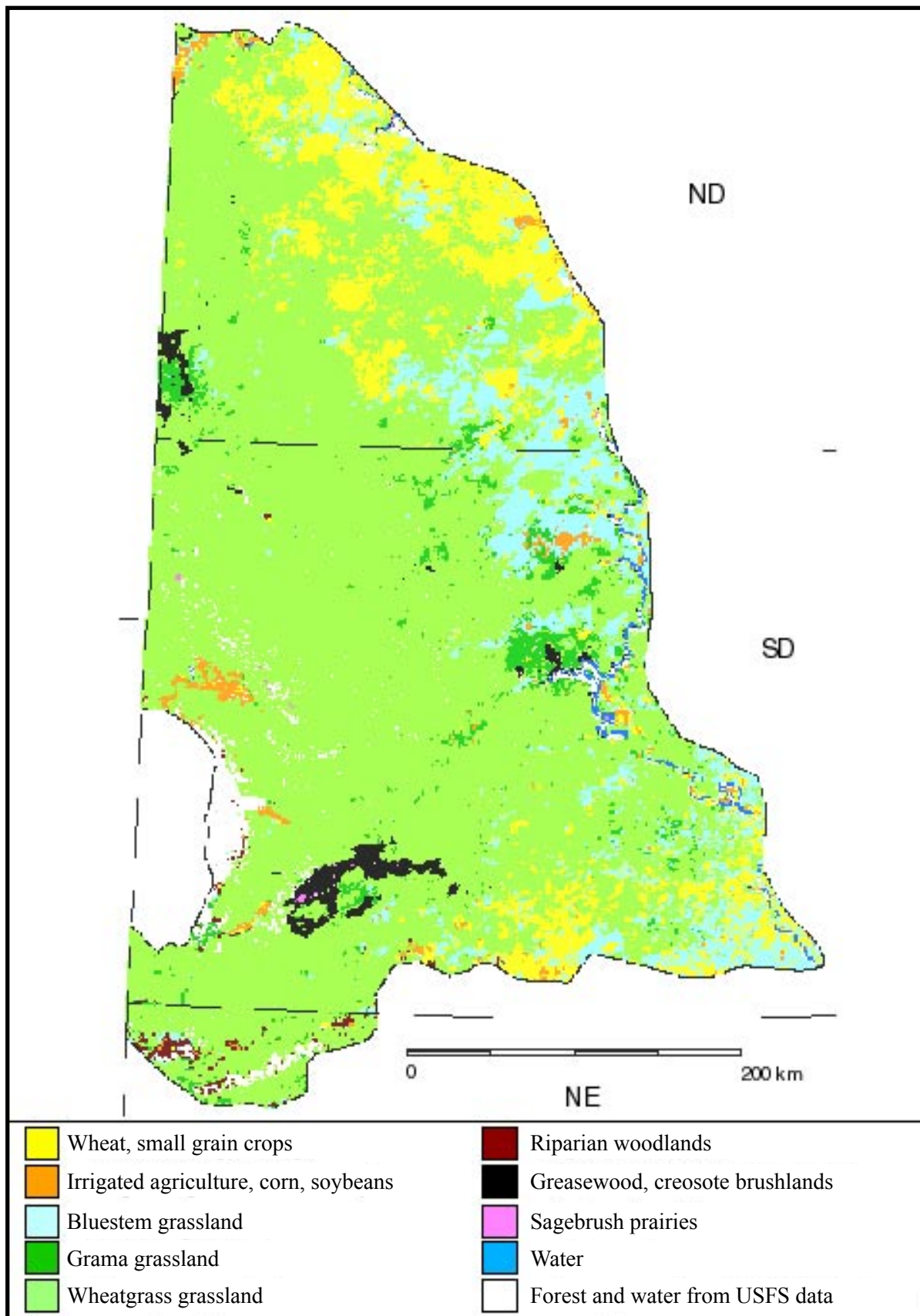


Figure 9. Distribution of major cover types in the 'Glaciated Missouri Plateau' physiographic area as estimated mostly with 1990 U.S. Geological Survey data and provided by Partners in Flight (<http://www.cast.uark.edu/pif/gif/38.nfor.gif>, December 1, 2004).

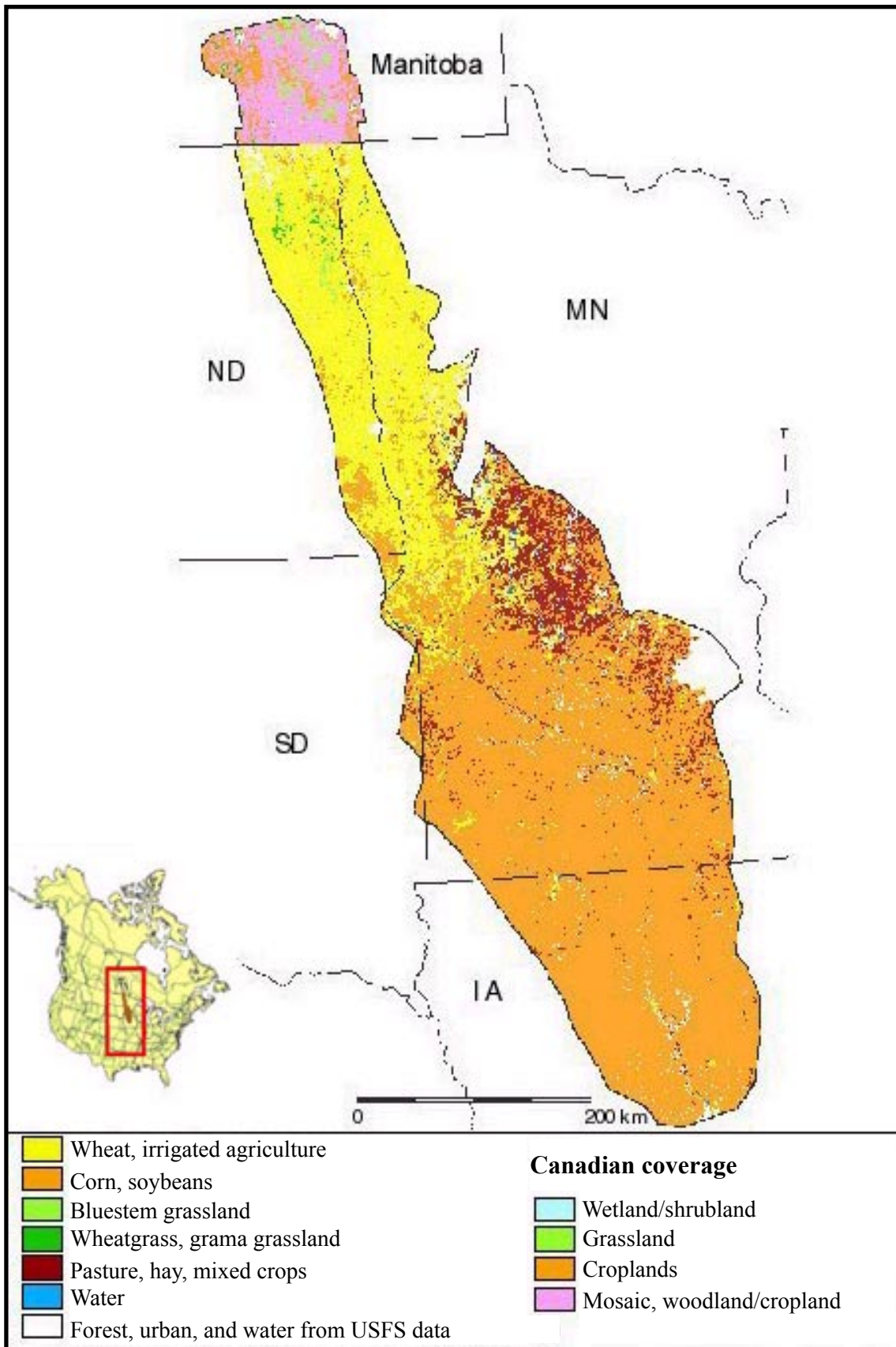


Figure 10. Distribution of major cover types in the 'Northern Tall Grass Prairie' physiographic area as estimated mostly with 1990 U.S. Geological Survey data and provided by Partners in Flight (http://www.blm.gov/wildlife/maps/pl_40map.gif, December 1, 2004).

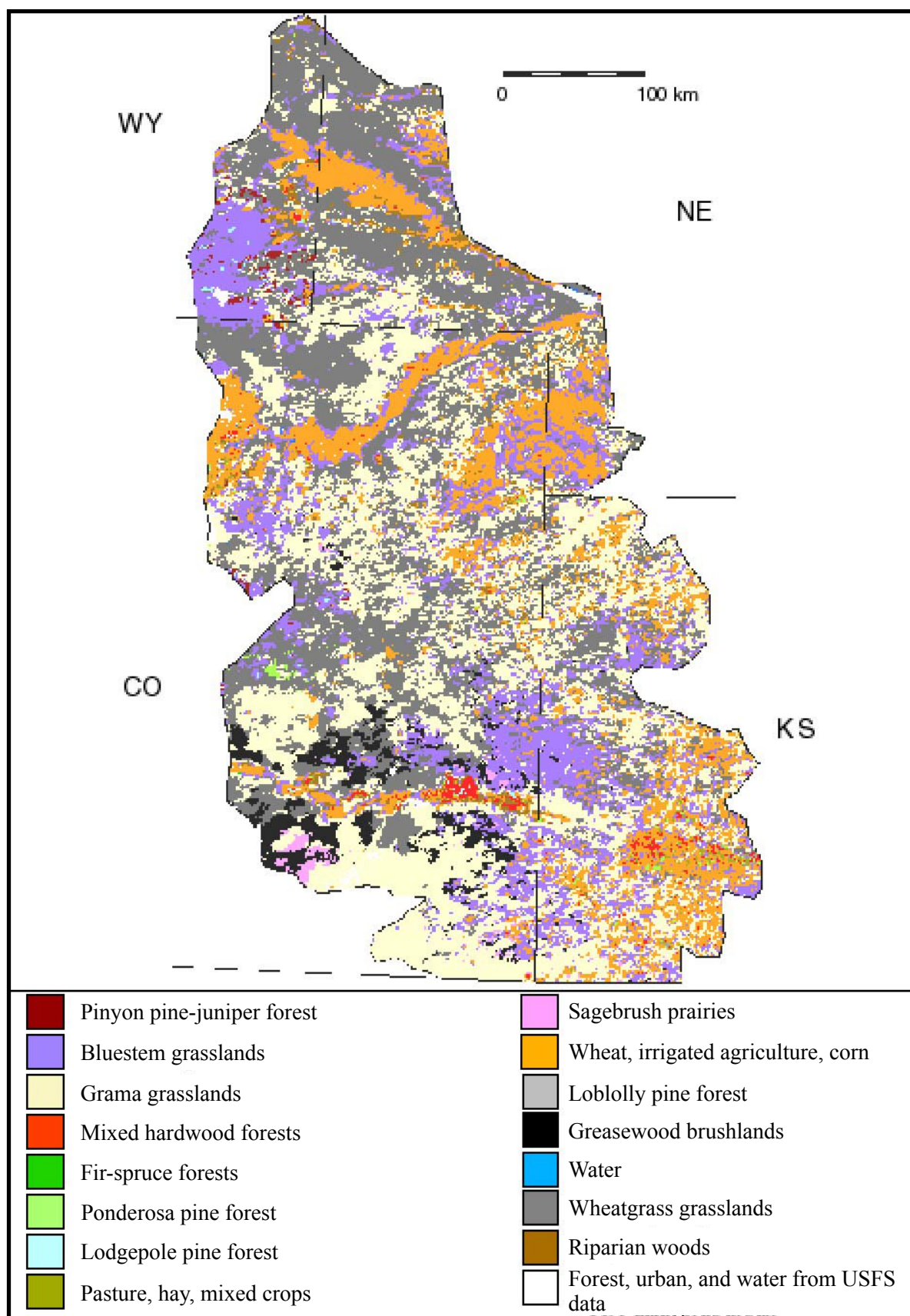


Figure 11. Distribution of major cover types in the 'Central Shortgrass Prairie' physiographic area as estimated mostly with 1990 U.S. Geological Survey data and provided by Partners in Flight (http://www.blm.gov/wildlife/maps/pl_36map.gif, December 1, 2004).

Table 1. Quantity of habitat types in USDA Forest Service Region 2 physiographic regions, as estimated with 1990 U.S. Geological Survey data and provided by Partners in Flight (<http://www.cast.uark.edu/pif/>, December 1, 2004).

Physiographic region	Grassland (%)	Shrubland (%)	Cropland (%)	Pasture/hay (%)	Forest (%)	Other (%)	Area (ha)
Central Shortgrass Prairie	77.9	3.7	14.5	0.3	3.2	0.4	17,055,668
Central-mixed Grass Prairie	57.9	0.0	40.3	1.1	0.5	0.2	22,107,300
Osage Plains	25.6	0.1	52.0	12.4	6.4	3.4	24,559,400
Dissected Till Plains	2.8	0.0	72.8	18.8	3.7	2.0	22,394,200
Northern Tallgrass Prairie	1.2	0.0	86.2	7.1	3.3	2.1	15,399,004
Northern Mixed Grass Prairie	18.5	0.0	75.7	0.3	4.1	1.3	30,270,489
Glaciated Missouri Plateau	81.9	1.6	12.9	0.0	2.6	1.1	15,623,853

as ‘unique’ when compared to habitat in other parts of the greater prairie-chicken’s range because of the prevalence of sand sagebrush (*Artemisia filifolia*) and small soapweed (*Yucca glauca*). The Sandhills are derived from windblown soils and elevations range from 1067 to 1372 m. Average annual precipitation is 46 cm, and temperature is 10 °C (range = -26 °C to 40 °C; Evans and Gilbert 1969). Dominant vegetation includes sand sagebrush with prairie sandreed, needle-and-thread, blue grama, and sand dropseed (*Sporobolus cryptandrus*). Other common grasses include sand bluestem, little bluestem, and switchgrass (**Figure 12**; Schroeder and Braun 1992a).

Habitat in Kansas

Populations of greater prairie-chickens are found in northern and eastern Kansas with the core of the distribution located in the tall-grass prairie of the Flint Hills region (Applegate and Horak 1999). Native grasses in this region include big bluestem (*Andropogon gerardi*), little bluestem, Indiangrass (*Sorghastrum nutans*), and switchgrass. Common forbs include leadplant (*Amorpha canescens*), blacksampson (*Echinacea angustifolia*), western ironweed (*Veronia baldwini*), broomweed (*Gutierrezia dracunculoides*), sunflower (*Helianthis* spp.), and goldenrod (*Solidago* spp.) (Horak 1985). In northeastern Kansas, Robel et al. (1970b) found that the ‘shallow range’ site was used most frequently despite representing only 16 to 21 percent of the study area; vegetation was predominately tall dropseed (*Sporobolus asper*), little bluestem, and big bluestem.

Lek habitat

Despite the variety of habitat types used by greater prairie-chickens, leks are typically located on elevated sites in open areas where the vegetation is short and sparse (**Table 2**). Cover type at the lek site appears to be “...incidental to the selection of open, relatively bare areas for courtship displays” (Christisen 1985: 26). Anderson (1969:643) observed experimental and natural changes in the cover types of 23 greater prairie-chicken leks in Wisconsin and concluded that “short cover and wide horizons, however, are physiognomic characteristics that were consistently preferred ...”. The mean height-density-index (VOR, a horizontal ‘visual obstruction reading’ measured in decimeters; Robel et al. 1970a) is generally low for lek sites; 63 percent of 800 readings were less than 0.5 dm for leks in the Flint Hills of Kansas (Horak 1985), and mean VOR for 65 leks in eastern Colorado was 0.1 dm (Schroeder and Braun 1992a). During the breeding season, males tend to loaf on or near the lek site. Consequently, loafing habitat in these situations is a reflection of vegetation near the lek.

Nest habitat

Female greater prairie-chickens construct nests that are shallow, bowl-shaped depressions in the substrate; they then line their nests with sparse amounts of dried grass, leaves, and feathers (**Figure 13**; Gross 1930, Hamerstrom 1939, Lehmann 1941). Specific features of nest sites vary among studies (**Table 3**), mainly because of geographic differences



Figure 12. Typical greater prairie-chicken habitat in northeastern Colorado consists of sand sagebrush and mid- and tallgrass prairie; yucca may also be present. Photograph by Michael A. Schroeder.

Table 2. Habitat features associated with greater prairie-chicken lek sites.

Region/state	Habitat type	Reference
Region 2		
South Dakota	Shortgrass	Evans (1968)
Nebraska	Wetland range sites with sparse vegetation	Kobriger (1965)
Kansas	“Droughty sites” and ridgetops with short sparse vegetation	Horak (1985)
Colorado	Low ridgetops with short sparse vegetation	Schroeder and Braun (1992a)
Other states		
North Dakota	Upland and midland grasslands in hummocky sandhills, short vegetation	Manske and Barker (1981, 1988)
Wisconsin	Plowed fields, pasture, hayfields with short or absent vegetation	Westemeier (1971)
Wisconsin	Open places, low knolls with cover of mixed grass, sedges, and forbs	Hamerstrom (1939)
Illinois	Elevated terrain and level bottoms of potholes with short vegetation	Yeatter (1943)
Missouri	Knolls with sparse vegetation, plowed fields and grassland	Christisen (1985)
Oklahoma	Shortgrass and midgrass sites on level prairie or elevations	Jones (1963)



Figure 13. Successful nest of a greater prairie-chicken in northeastern Colorado. Photograph by Michael A. Schroeder.

in habitat, variations in sampling methodology, and timing of measurements in relation to nest initiation (Buhnerkempe et al. 1984, Svedarsky and Van Amburg 1996). Despite these variations, nests tend to be located in habitats with dense residual cover that provides vertical and horizontal concealment (Horak 1985 in Kansas, Schroeder and Braun 1992a in Colorado, Manske and Barker 1988 in North Dakota, Rice and Carter 1982 in South Dakota, Svedarsky 1988 in Minnesota). Horak (1985:44) believed that residual vegetation was “critical” for nest concealment, and Manske and Barker (1988:16) found that nest sites in their study were “...completely covered by vegetation.”

Buhnerkempe et al. (1984) compared vegetation structure of fields in Illinois and concluded that nests were found in fields with greater vegetation height and cover. Females selected nesting habitat with dense cover in eastern Colorado; 46 percent of 83 nest sites were in areas dominated by prairie sandreed, even though this habitat type accounted for only 17 percent of the

study area (Schroeder and Braun 1992a). Similarly in Minnesota, Svedarsky (1988) found 22 percent of 36 nest sites were in smooth brome (*Bromus inermis*), a grass habitat type that comprised only 3 percent of the study area. In Missouri, 17 percent of 35 nests were located in legume fields, which accounted for only 1 percent of their study area (Drobney and Sparrowe 1977), and in southern Illinois Yeatter (1943) located 33 percent of 39 nests in waste grassland, which accounted for 4 percent of the total nesting cover.

Kirsch (1974) believed that throughout the geographic range of greater prairie-chickens, high quality nesting habitat consisted of grasslands where residual vegetation averaged 50 cm during spring and was dense enough to conceal a nest. Svedarsky and Van Amburg (1996:3), citing R. L. Westemeier’s 26 year study of greater prairie-chickens in Illinois (habitat data for over 1000 nest sites), concluded that “...nesting cover should be relatively dense close to the ground, about 40 cm tall, and have a growth form similar to

Table 3. Nest site features for greater prairie-chickens.

State	Vegetation height (cm)	Dominant species	General characteristics	Nests (n)	Study
South Dakota	Not given	<i>Stipa viridula</i> , <i>Agropyron smithii</i>	Residual vegetation rolling range sites	36	Rice and Carter (1982)
Nebraska	13	<i>Andropogon scoparius</i> , <i>Eragrostis trichodes</i>	Not given	2	Blus and Walker (1966)
Kansas	29	<i>Andropogon</i> sp.	Well drained sites in open areas, no trees	20	Horak (1985)
Colorado	59 VOR ^a	<i>Calamovilfa longifolia</i>	Not given	83	Schroeder and Braun (1992a)
North Dakota	29 VOR ^a	<i>Panicum virgatum</i>	Dense vertical and horizontal cover	11	Manske and Barker (1988)
North Dakota	16 (effective height)	<i>Andropogon scoparius</i> , <i>Poa pratensis</i>	Not given	62	Newell et al. (1988)
Minnesota	20 VOR ^a	<i>Andropogon gerardi</i> , <i>Bromus inermis</i>	Undisturbed for one growing season	36	Svedarsky (1988)
Michigan	Not given	Not given	Grassland in open areas	13	Ammann (1957)
Illinois	20 VOR ^a	<i>Bromus</i> sp., redtop, timothy	Not given	18	Westeimeier et al. (1995)
Missouri	45	<i>Andropogon scoparius</i>	Not given	23	Drobney and Sparrowe (1977)
Oklahoma	45	<i>Andropogon scoparius</i>	Not given	9	Jones (1963)

^aVOR refers to the visual obstruction reading on a Robel pole (Robel et al. 1970a).

smooth brome.” The key structural features of grasses in nesting habitat include a majority of leaves along the stem rather than at the base, an average VOR of approximately 2.7 dm, and a growth form resistant to flattening by snow cover. Svedarsky and Van Amburg (1996:4) believed that “...plant species composition [of nesting habitat] in itself is not important so long as density requirements are met...”

In some cases, increased litter depth (horizontally-orientated residual vegetation near the ground) has been related to decreased nest success (Svedarsky 1988, McKee et al. 1998). Svedarsky (1988) suggested that habitats with increased litter depth may support higher numbers of small mammals, which, in turn, may affect predator use resulting in higher nest predation for ground nesting birds. Although Svedarsky (1988) did not record a threshold level for litter depth, McKee et al. (1998) found that nest success declined when nest litter cover exceeded 25 percent of total ground cover in an intensively managed tallgrass prairie of southwestern Missouri. Horak (1985) also believed that greater prairie-chickens could not tolerate “too much duff”, but

he did not indicate what “too much duff” would be. It should be noted that studies documenting a relationship between litter depth and nest success have generally been conducted in the eastern part of the range of greater prairie-chickens. These areas typically receive higher levels of precipitation than Region 2, where precipitation may be limiting (Svedarsky et al. 2000). A negative relationship between litter depth and nest success may not apply to drier grassland communities, or areas where grazing is a major land use practice (McKee et al. 1998).

Raptors, owls, and corvids are predators of both nests and chicks (Schroeder and Robb 1993), and the presence of woody vegetation may provide hunting perches for these birds. Abundance of shrubs/woody vegetation within 50 m of the nest site was significantly higher for unsuccessful nests than successful nests in Minnesota, even though VOR readings of the nest sites were similar (Svedarsky 1988). In Missouri, 18 percent of 17 nests hatched in habitats where woody cover was greater than 5 percent while 58 percent of 26 nests hatched when woody cover was less than 5 percent (McKee et al. 1998).

Summer habitat

Brood habitat must be structured so that chicks can travel easily; it must provide adequate protection from predators and weather, and it must supply the nutritional resources necessary for both the female and her chicks (Svedarsky 1988). Early studies of brood habitat essentially described areas where broods were found during field searches or chance encounters (Gross 1930, Lehmann 1941, Yeatter 1943, Jones 1963, Kobriger 1965, Drobney and Sparrowe 1977, Horak 1985). Later studies monitored radio-tagged females to obtain a clearer (less biased) picture of both local and broad-scale habitat use by broods (Newell et al. 1988, Svedarsky 1988).

Although many different vegetation associations are used throughout the distribution of greater prairie-chickens, disturbance is a common characteristic of brood habitat (Jones 1963 – Oklahoma, Rice and Carter 1982 – South Dakota, Horak 1985 – Kansas, Newell et al. 1988 – North Dakota, Manske and Barker 1988 – North Dakota, Svedarsky 1988 – Minnesota, Westemeier et al. 1995 – Illinois). For instance, Svedarsky (1988: 224) found that “after hatching, broods generally moved directly from undisturbed cover surrounding nests to habitats that had been disturbed.” In this case, the disturbed habitat was bluestem grasslands that had been burned, grazed, or hayed the previous year. Newly seeded grass-legumes, recently burned brome, and weeds with scattered legumes have been used in Illinois (Westemeier et al. 1995) as well as redtop (*Agrostis alba*) fields, small grains, and grassy fallow fields (Yeatter 1943). Prairie hay fields and pastures were used by broods in a large tract of native grassland near Taberville, Missouri (Burger et al. 1989), and Horak (1985) observed more broods in cultivated or disturbed areas than in large tracts of native pasture in Kansas. Similarly, Jones (1963) noted that cultivated pasture, dominated by low weeds and annual *Lespedeza*, was the vegetation association most frequently used by broods in northern Osage County, Oklahoma.

Lehmann (1941:16) observed females leading their broods from the nest and noted that they “...traveled through the lightest cover or followed trails...” In Kansas, broods were most commonly found in “...areas that were easy to walk through, but with sufficient vegetation to provide security” (Horak 1985: 48). In North Dakota (Sheyenne National Grassland), broods foraged in areas that had been mowed or grazed, and used adjacent areas of dense vegetation for loafing and escape cover (Manske and Barker 1988). Manske and Barker (1988) considered good concealment cover

for greater prairie-chickens to have a mean VOR greater than 1.5 dm (VOR follows Robel et al. 1970a). These areas also had greater amounts of short shrubs and forbs, and they characteristically provided “...good canopy cover and relatively open understories” (Manske and Barker 1988:17). Broods in Colorado used areas with taller vegetation (Schroeder and Braun 1992a), and in North Dakota Newell et al. (1988) found brood females selecting tall vegetation (26 to 50 cm) 81.8 percent of the time throughout the summer.

Many studies report extensive use of lowland areas by broods. Newell et al. (1988) found higher use of lowland areas by broods, especially during June when the vegetation was taller and denser, than the more heavily grazed upland. Wetland meadows were used throughout the day by broods in Nebraska (Valentine National Wildlife Refuge), and during the heat of mid-day birds loafed in available shade provided by tall, unmowed vegetation (Kobriger 1965). In South Dakota (Fort Pierre National Grassland) during a severe drought, broods made intensive use of unmowed roadside ditches and areas surrounding stock tanks (Rice and Carter 1982). In years preceding and following the drought, sweet clover (*Melilotus officinalis*), snowberry (*Symphoricarpos albus*), western wheatgrass, and green needlegrass were commonly used as cover, and broods were often found in vegetation along drainages. Legume fields accounted for 19 percent of 139 brood observations in Missouri even though they comprised only 1 percent of the study area (Drobney and Sparrowe 1977). Similar findings were reported in North Dakota, where alfalfa fields and prairie hay adjacent to or containing alfalfa accounted for 65 percent of the 20 heavily used brood sites (Newell et al. 1988).

Schroeder and Braun (1992a) found that species richness (plant diversity) was significantly greater in brood habitat. Jones (1963:773) surveyed insect densities in various habitats and concluded that “...the vegetation with the greater percentage of forbs consistently had more insects per unit area...” High grasshopper densities, in habitats with a VOR ranging from 2.0 to 4.0 dm, are associated with quality brood habitat in Illinois (Westemeier et al. 1995). Burger et al. (1989:14) refers to “...hens at Taberville frequently [taking] their broods to forage in insect-rich prairie hay fields and pasture.” And Horak (1985) attributed the use of disturbed areas by broods to greater insect abundance in diverse habitats.

Daytime loafing areas during the summer are often associated with shrubs that provide shade (Manske and Barker 1988). In North Dakota, shade from leadplant

in the uplands and willow (*Salix* spp.) in lowland areas was commonly used by birds for loafing areas during the hottest part of the day (Manske and Barker 1988). Yeatter (1943) observed broods loafing in the shade of trees, small shrubs, fence-lines, hedges, and cornfields. In eastern Colorado, birds commonly loafed in the shade of sand sagebrush during mid-summer, and sometimes rested in shallow depressions they had scraped in the soil (Schroeder and Robb 1993). Habitat at these sites generally had taller sand sagebrush (mean = 68 cm), grass (mean = 108 cm), and forbs (mean = 68 cm) than foraging areas (Schroeder and Braun 1992a, *n* = 90). In Missouri, birds primarily roosted in prairie pasture (88 percent of 1180 observations), especially in areas where the vegetation ranged in height from 20 to 90 cm (Drobney and Sparrowe 1977).

Autumn and winter habitat

During the fall and winter, greater prairie-chickens usually feed in the mornings and evenings, loaf (rest) during the middle of the day, and roost at night. Crop fields are often used for feeding (Schroeder and Robb 1993). Manske and Barker (1988:17) found that birds spent a large part of the daytime loafing, leading them to conclude that "Roosting activity occupied the greatest amount of time in the life of a prairie grouse." As roosting/loafing habitat offers concealment from predators and protection from the elements, it may differ seasonally.

A comprehensive study of winter loafing/roosting behavior and habitat was conducted on 3,945 observations of 22 radio-marked greater prairie-chickens on the Shewyenne National Grasslands, North Dakota by Toepfer and Eng (1988). They determined that most day roosting areas were in grasslands where vegetation height was greater than 25 cm. However, greater prairie-chickens would also loaf in agriculture habitat (corn, oats, sunflowers). Night roosts (*n* = 525) were located in grassland (67 percent), shrubland (12 percent), and wetland (7 percent) sites, generally where the vegetation height was 26 to 50 cm, or greater. Areas used for night roosts were open, relatively large, and undisturbed. Within the grassland habitat, unmowed and lightly grazed lowland sites were most commonly used. Toepfer and Eng (1988) categorized winter roosts into four types: 1) vegetation roost (cover provided by vegetation), 2) snow depression (cover provided by snow), 3) snow-vegetation roost (cover provided by snow and vegetation), and 4) snow burrow (a tunnel into soft snow). Nearly all roost sites they located were associated with vegetation, primarily grasses and sedges (74 percent). Night roosts were nearly always located

in areas of greater total cover (snow or vegetation or combination) and deeper snow. Greater prairie-chickens made snow burrows in areas of tall vegetation that accumulated and held snow cover; areas of dense vegetation were not used, possibly because birds had difficulty burrowing in sites with high stem density. When snow burrows collapsed, or when conditions were not favorable, greater prairie-chickens made snow depressions, often forming as many as three snow depressions before remaining at a final roost site.

Mohler (1952:15) examined winter loafing/roosting behavior of greater prairie-chickens in Chase County, Nebraska and Yuma County, Colorado and determined that loafing/roosting habitat consisted of grassland sites having the following characteristics: "(1) numerous stems over two feet in height, (2) fairly dense cover extending from one to two feet above the ground, and (3) a dense understory of fallen and tangled grasses covering the ground to a depth of eight inches or more." Mohler (1952) found that roosting habitat generally consisted of sand sagebrush, commonly interspersed with prairie sandreed.

Landscape configuration

Several studies have emphasized the importance of nesting and brood-rearing habitat (Hamerstrom et al. 1957, Kirsch 1974) while others have shown the necessity of winter foraging and roosting habitat (Toepfer and Eng 1988). Most agree that although these habitats are important, it is the interrelatedness of habitat quality, quantity, and configuration that is crucial for greater prairie-chickens. For instance, in Nebraska, outside of the Sandhills, populations are highest where the habitat is 70 percent grassland and 30 percent cropland (Vodehnal 1999) but decline as the proportion of grassland to cropland decreases. Svedarsky et al. (2000:277) suggested that the peak in historical abundance of greater prairie-chickens occurred "...when cropland was 20 – 30% of the grassland landscape, but declined when the cropland proportion exceeded that." Populations in Colorado are on the periphery of the geographic distribution of greater prairie-chickens where rangeland (85 percent) is interspersed with center-pivot corn circles (13 percent). In this area, it is the "disjunct configuration" of cropland to rangeland in a configuration suitable for greater prairie-chickens that is important (Schroeder and Braun 1992a, Westemeier and Gough 1999:170). Similar findings regarding the importance of a mixture of cropland and grasslands have been reported for other parts of this species' range (Yeatter 1943 – Illinois, Arthaud 1970 – Missouri, Hamerstrom and Hamerstrom 1973 – Wisconsin,

Kirsch et al. 1973 – North Dakota, and Applegate and Horak 1999 – Kansas).

Throughout the geographic range of greater prairie-chickens, there is a correlation between lek locations and nest sites, with most nests located within 1.6 km of the nearest lek (Yeatter 1943 – Illinois, Jones 1963 – Oklahoma, Robel 1970 – Kansas, Drobney and Sparrowe 1977 – Missouri, Horak 1985 – Kansas, Svedarsky 1988 – Minnesota, Schroeder 1991 – Colorado). However, it is also possible that there is a correlation between habitat characteristics and distance to the nearest lek (Schroeder and Braun 1992). Moreover, males are known to use a wide variety of habitats, including bare ground, for lekking, but nesting habitat may be limiting for females. It may be that lek sites generally form in areas of high female traffic, i.e. near substantial nesting habitat (Schroeder and White 1993). One complicating factor is that some females may move more than 20 km from a lek where they were captured to their nest site (Schroeder 1991).

Females move their broods soon after hatch, usually to insect-rich habitats. Young broods are unable to fly; therefore suitable brood habitat for foraging and concealment has to be within walking distance of the nest. Although broods are capable of traveling considerable distances (Svedarsky 1988), such movements may increase energy expenditure by chicks and exposure to predation (Newell et al. 1988). Broods often use relatively small, localized areas of their home range for several days at a time, and they are known to relocate to new areas following disturbance and/or predation attempts on chicks (Newell et al. 1988, Svedarsky 1988). Broods in a mixed agriculture-prairie habitat were found to travel greater daily distances than broods using more contiguous prairie habitat (Ryan et al. 1998).

Greater prairie-chickens move to wintering areas during autumn, but some birds, such as unsuccessful brood females, may move during mid-summer (Schroeder and Braun 1993). Although birds can move long distances to wintering sites, most remain relatively close to their breeding areas; in eastern Colorado, 65 percent of females and 95 percent of males wintered less than 5 km from their breeding territories (Schroeder and Braun 1993). Once established on a wintering site, birds tend to form flocks that exhibit relatively small home ranges. For instance, a territorial male may remain within 3 km of his home lek throughout the winter, and travel, at most, 1.6 km between roosting and foraging areas (Toepfer and Eng 1988). Ready access to an adequate winter food source and suitable roosting cover

are believed to be important habitat features in parts of the geographic distribution of greater prairie-chickens that receive snow during winter (Christisen 1969). Extensive daily movements to winter food sources may expose greater prairie-chickens to increased predation and be energetically more costly. Low survival of radio-marked greater prairie-chickens translocated within South Dakota was attributed to lack of winter food at some release sites and lack of adequate grassland roosting cover at others (Fredrickson et al. 1999).

Occupied versus unoccupied habitat

Greater prairie-chickens are a grassland-dependent species whose distribution and abundance are closely associated with land use practices (Giesen and Schroeder 1999). At one time they were found as far north as central Alberta, south to Texas, west to northeastern Colorado, and east to southern Ontario and Ohio (**Figure 2**; Aldrich and Duvall 1955). Their versatility is illustrated by the former abundance of the heath hen in the northeastern states and the Attwater's prairie-chicken in southern Texas and Louisiana. Currently, "Loss of habitat suitable for successful nesting and brood rearing is the single most important factor leading to declines, isolation, and extirpations throughout the species' range in the midwestern United States" (Westemeier et al. 1998:1695). Greater prairie-chickens are found primarily on private lands, and as such, they are affected by the economics of land management practices; in the eastern part of their range, the substantial amounts of grassland required by greater prairie-chickens are also valuable cropland (Svedarsky et al. 2000). At one time, more than 60 percent of Illinois supported greater prairie-chickens; currently less than 0.01 percent of the native tallgrass prairie remains, and populations of greater prairie-chickens are few, small, and isolated (Westemeier et al. 1998). Conservation efforts for greater prairie-chickens may have more success in the western part of this species' range as the primary land use practice is grazing, which keeps large areas of rangeland intact (Svedarsky et al. 2000). However, in many cases, land use practices such as heavy grazing and annual burning reduce the quality and hence the availability of greater prairie-chicken habitat (**Figure 14**).

Habitat that could support greater prairie-chickens is not always occupied. In an effort to expand the distribution of greater prairie chickens in Colorado, the Colorado Division of Wildlife translocated greater prairie-chickens to the Tamarack State Wildlife Area in Logan County. This area was part of the historical range of greater prairie-chickens in Colorado, but birds had



Figure 14. The effects of grazing practices on greater prairie-chicken habitat. The heavily grazed field at the right is less likely to support nesting and brood-rearing by greater prairie-chickens. Photograph by Michael A. Schroeder.

not been observed there since 1963, even though the core of the greater prairie-chicken distribution in this state was only 32 km away (Hoffmann et al. 1992). The Flint Hills of Kansas have traditionally supported the best populations of greater prairie-chickens in this state. In recent years there has been an increase in annual burning of entire pastures, a practice that eliminates residual vegetation crucial for nesting, and heavy grazing during early spring (Applegate and Horak 1999). Since 1982, there has been a downward trend in greater prairie-chicken numbers.

Food habits

Diet items

Composition of greater prairie-chicken diet varies among regions, seasons, and age classes (**Table 4** and **Table 5**). In part, these differences result from variation in food availability and habitats. Their diet is primarily comprised of cultivated grains, leaves, seeds, buds, and insect material (**Table 4**; Yeatter 1943, Mohler 1952, Korschgen 1962, Jones 1963, Rumble et al. 1988). A wide array of vegetation is consumed, as many as

161 different plant species, although as few as 10 may comprise the bulk of the diet (Korschgen 1962). Greater prairie-chickens typically forage on the ground but have been observed to eat the buds of a variety of woody plants such as birch (*Betula* spp.) and aspen (*Populus* spp.) during the winter when snow cover reduces the availability of other foods (Schmidt 1936, Hamerstrom et al. 1941, Grange 1948, Horak 1985). Although greater prairie-chickens may feed throughout the day, most feeding occurs during a 2-hour period around sunrise and a 1 hour period near sunset (Yeatter 1943, Baker 1953, Horak 1985).

The relative importance of agricultural grains in the diet of greater prairie-chickens appears to have increased from historical to present time (Hamerstrom et al. 1941). Leopold (1931) reviewed historical accounts of greater prairie-chicken observations and concluded that much of the range in the northern states was acquired, not original. He attributed the northern expansion of greater prairie-chickens to their ability to use corn as a food source in a landscape where agriculture was replacing native grassland. The value of grains in the diet is illustrated by Hamerstrom et

Table 4. Diet items (percent of total volume) for four studies of greater prairie-chickens.

Food item(s)	Dec-Feb		Mar-May		Jun-Aug			Sep-Nov	
	a	b	a	b	a	b	c	a	d
<i>Zea mays</i>	45.6	50.7	48.8	18.1	5.2	2.2	—	23.5	14.9
<i>Glycine max</i>	2.6	5.6	8.7	—	28.3	—	—	8.6	—
<i>Sorghum vulgare</i>	21.4	—	9.3	—	0.1	—	—	22	22.2
<i>Panicum</i> sp.	—	—	—	—	—	—	—	—	Trace
<i>Lespedeza stipulacea</i>	4.3	—	3.0	—	20.5	—	—	15.2	9.4
<i>Soya max</i>	—	—	—	—	—	—	—	—	7.6
<i>Strophostyles leiosperma</i>	—	—	—	—	—	—	—	—	1.7
<i>Medicago sativa</i>	—	—	—	—	—	—	—	—	0.3
<i>Medicago/Melilotus</i> spp.	—	—	—	25.6	—	29.4	—	—	—
<i>Oxalis</i> sp.	—	—	—	—	—	—	—	—	Trace
Miscellaneous plant material	8.9	—	7.3	9.0	7.9	7.2	0.9	4.3	12.6
<i>Triticum aestivum</i>	1.2	—	Trace	—	15.9	—	—	6.6	15.3
<i>Triticum sativum</i>	—	—	—	—	—	—	4.7	—	—
Green grass	7.0	—	6.7	—	1.9	—	—	3.6	—
<i>Avena sativa</i>	0.5	—	1.3	—	4.8	—	—	4.6	1.6
<i>Carex</i> spp.	Trace	—	6.1	0.5	0.4	1.6	—	Trace	—
<i>Ambrosia artemisiifolia</i>	0.8	—	Trace	—	0.0	—	—	3.8	—
<i>Rosa</i> spp.	2.0	—	0.4	0.2	2.1	0.8	—	1.5	0.9
<i>Rosa setigera</i>	—	—	—	—	—	—	1.1	—	—
<i>Rosa multiflora</i>	0.6	—	2.8	—	0.0	—	—	Trace	—
<i>Coreopsis grandiflora</i>	0.0	—	0.0	—	3.0	—	—	0.0	—
<i>Festuca elatior</i>	0.0	—	Trace	—	2.9	—	—	0.0	—
<i>Ambrosia trifida</i>	—	—	—	—	—	—	9.0	—	0.2
<i>Ambrosia bidentata</i>	1.7	—	Trace	—	0.0	—	—	1.4	1.1
<i>Ambrosia</i> sp.	—	—	—	0.5	—	1.5	—	—	1.0
<i>Helianthus annuus</i>	—	8.8	—	—	—	—	—	—	0.4
<i>Ranunculus fascicularis</i>	0.0	—	3.1	—	0.2	—	—	0.0	—
<i>Rhus copallina</i>	1.5	—	0.6	—	0.1	—	—	0.2	—
<i>Rhus</i> sp.	—	—	—	—	—	—	—	—	1.6
<i>Serinia oppositifolia</i>	0.0	—	2.0	—	0.1	—	—	0.0	—
<i>Trifolium repens</i>	—	—	—	—	—	—	—	—	1.5
<i>Trifolium</i> spp.	Trace	—	0.9	—	0.5	—	—	0.1	—
<i>Taraxacum officinale</i>	0.0	—	1.6	16.7	Trace	9.3	—	0.0	—
<i>Oenothera linifolia</i>	Trace	—	Trace	—	1.4	—	—	Trace	—
<i>Veronica peregrina</i>	0.0	—	1.4	—	Trace	—	—	0.0	—
<i>Cerastium vulgatum</i>	0.0	—	0.7	—	0.4	—	—	0.0	—
<i>Polygonum pensylvanicum</i>	0.4	—	Trace	—	0.1	—	0.8	0.6	—
<i>Polygonum</i> sp.	—	—	—	—	—	—	—	—	Trace
Unidentified roots	Trace	—	Trace	—	Trace	—	—	0.8	—
<i>Antennaria neglecta</i>	0.0	—	2.1	—	0.0	—	—	Trace	—
<i>Antennaria/Cersium</i> spp.	—	—	—	2.1	—	0.1	—	—	—

Table 4 (concluded).

Food item(s)	Dec-Feb		Mar-May		Jun-Aug			Sep-Nov	
	a	b	a	b	a	b	c	a	d
<i>Hordeum vulgare</i>	0.1	—	0.0	—	0.0	—	—	0.7	—
<i>Rubus</i> spp.	0.0	—	0.0	—	0.6	—	—	Trace	—
<i>Silene antirrhina</i>	0.0	—	Trace	—	0.5	—	—	0.0	—
<i>Cyperus</i> sp.	—	—	—	—	—	—	—	—	Trace
<i>Vitis</i> sp.	—	—	—	—	—	—	—	—	Trace
<i>Abutilon theophraste</i>	—	—	—	—	—	—	—	—	Trace
<i>Hibiscus trionum</i>	—	—	—	—	—	—	—	—	2.2
<i>Cornus paniculata</i>	—	—	—	—	—	—	3.4	—	0.5
<i>Ruellia</i> sp.	—	—	—	—	—	—	—	—	0.3
<i>Diodea teres</i>	—	—	—	—	—	—	21.2	—	Trace
<i>Symphoricarpos orbiculatus</i>	—	—	—	—	—	—	—	—	0.3
<i>Poa pratensis</i>	—	—	—	0.9	—	0.3	—	—	—
<i>Artemesia frigida</i>	—	4.9	—	8.3	—	0.5	—	—	—
<i>Agropyron</i> spp.	—	—	—	0.1	—	Trace	—	—	—
<i>Andropogon</i> spp.	—	—	—	Trace	—	0.2	—	—	—
<i>Eleocharis</i> spp.	—	—	—	0.2	—	0.2	—	—	—
<i>Equisetum</i> spp.	—	—	—	0.3	—	Trace	—	—	—
<i>Cassia chamaecrista</i>	—	—	—	—	—	—	4.6	—	—
<i>Brassica</i> sp.	—	—	—	—	—	—	Trace	—	—
<i>Convolvulus</i> sp.	—	—	—	—	—	—	Trace	—	—
<i>Setaria glauca</i>	—	—	—	—	—	—	Trace	—	—
<i>Prunus serotina</i>	—	—	—	—	—	—	2.0	—	—
<i>Crataegus</i> sp.	—	—	—	—	—	—	Trace	—	—
<i>Euphorbia corollata</i>	—	—	—	—	—	—	9.3	—	—
<i>Solidago</i> sp.	—	—	—	—	—	—	7.5	—	—
Grass seeds	—	11.2	—	0.7	—	0.3	—	—	—
Forb seeds	—	10.1	—	1.1	—	1.1	—	—	—
Unknown forbs	—	5.7	—	0.9	—	1.2	—	—	—
Unknown shrubs	—	1.3	—	0.5	—	Trace	—	—	—
Unknown grasses	—	1.5	—	0.5	—	0.5	—	—	—
Acorns	—	—	—	—	—	—	0.5	—	—
Orthoptera	—	—	—	—	—	—	4.8	—	0.2
Coleoptera	—	—	—	—	—	—	4.0	—	Trace
Hemiptera	—	—	—	—	—	—	—	—	Trace
Homoptera	—	—	—	—	—	—	—	—	0.1
Lepidoptera	—	—	—	—	—	—	0.1	—	Trace
Unknown insects	—	—	—	7.2	—	41.7	0.1	—	—

^aKorschgen 1962: Missouri – fecal droppings $n = 5040$.

^bRumble et al. 1988: Sheyenne National Grasslands, North Dakota – fecal droppings; Dec-Feb $n = 119$, Mar-May $n = 133$, Jun-Aug $n = 110$.

^cYeatter 1943: Illinois – stomach contents $n = 10$.

^dBaker 1953: Kansas – crop contents $n = 29$, gizzard contents $n = 20$.

Table 5. Major dietary items for juvenile greater prairie-chickens. Values represent percent of total volume (sample sizes for each study in parentheses).

Food item(s)	June		July	August	Jun-Aug
	^a (15)	^b (14)	^a (30)	^a (30)	^c (14)
<i>Lespedeza stipulaceae</i>	—	1.2	—	—	—
<i>Sabatia campestris</i>	—	Trace	—	—	—
<i>Panicum capillare</i>	—	Trace	—	—	—
<i>Taraxacum officinale</i>	0.0	—	3.5	1.5	—
<i>Medicago/melilotus</i> spp.	7.4	—	2.9	4.5	—
<i>Artemisia frigida</i>	0.1	—	0.2	0.1	—
<i>Poa pratensis</i>	0.7	—	0.6	0.4	—
<i>Carex</i> spp.	5.6	—	2.0	0.3	—
<i>Equisetum</i> spp.	0.6	—	0.3	0.0	—
<i>Eleocharis</i> spp.	3.3	—	0.7	0.0	—
<i>Andropogon</i> spp.	0.0	—	0.2	0.1	—
<i>Ambrosia</i> spp.	0.0	—	0.1	0.2	—
<i>Agropyron</i> spp.	0.1	—	0.1	0.2	—
<i>Rubus villosus</i>	—	—	—	—	13.2
<i>Prunus serotina</i>	—	—	—	—	6.1
<i>Cornus paniculata</i>	—	—	—	—	2.8
<i>Rosa setigera</i>	—	—	—	—	0.4
<i>Physalis</i> sp.	—	—	—	—	0.1
<i>Crataegus</i> sp.	—	—	—	—	Trace
<i>Triticum sativum</i>	—	—	—	—	17.3
<i>Zea mays</i>	—	—	—	—	1.6
<i>Avena sativa</i>	—	—	—	—	Trace
<i>Diodia teres</i>	—	—	—	—	11.8
<i>Paspalum</i> sp.	—	—	—	—	0.2
<i>Panicum huachucae</i>	—	—	—	—	Trace
<i>Rumex acetosella</i>	—	—	—	—	Trace
<i>Polygonum aviculare</i>	—	—	—	—	Trace
<i>Setaria glauca</i>	—	—	—	—	Trace
<i>Solidago</i> sp.	—	—	—	—	2.9
Unknown forbs	0.1	—	0.4	0.0	—
Unknown grasses	1.6	1.1	1.0	0.8	—
Unknown shrubs	0.1	—	0.1	0.2	—
Plant material	0.1	—	0.7	1.9	3.5
Coleoptera	—	21.9	—	—	13.6
Orthoptera	—	7.4	—	—	21.7
Hemiptera	—	0.7	—	—	1.3
Neuroptera	—	0.6	—	—	—
Homoptera	—	0.7	—	—	Trace
Hymenoptera	—	0.2	—	—	0.9
Diptera	—	—	—	—	0.7
Lepidoptera	—	—	—	—	0.4
Arachnids	—	—	—	—	0.9
Unknown insects	80.1	66.2	87.3	86.3	—
Total insects	80.1	97.7	87.3	86.3	39.5

^aRumble et al. 1988: Sheyenne National Grasslands, North Dakota - fecal droppings.

^bJones 1963: Oklahoma - fecal droppings.

^cYeatter 1943: Illinois - stomach contents.

al. (1941) who determined from experimental feeding trials that birds fed a diet of browse lost significant weight and in some cases died of starvation. They concluded that "...browse alone will not carry greater prairie-chickens through the winter. Small numbers may be able to supplement a browse diet with an uncertain supply of weed seeds, but to have greater prairie-chickens in quantity in the North Central States, winter grains are necessary." (Hamerstrom et al. 1941: 192). Much of the current distribution of greater prairie-chickens is located in acquired range; in many cases, these areas did not originally support populations of greater prairie-chickens (Schroeder and Robb 1993), thus the presence of suitable cultivated grains is likely important (Westemeier and Gough 1999).

Cultivated grains constitute a significant proportion of the autumn/winter diet of greater prairie-chickens throughout their range. Greater prairie-chickens commonly eat corn, soybeans, sorghum, and wheat, when available; these grains can comprise anywhere from 34 to 71 percent of their diet (**Table 6**). Lehmann (1941) however, examined crop contents and fecal droppings from Attwater's prairie-chickens in Texas and concluded that native plants were the most commonly eaten foods, and cultivated grains, although available, constituted a small proportion of the diet. This suggests that grains in the diet may be more important in areas of colder temperatures and greater snow cover. Grange (1948:160) noted for birds in Wisconsin "...The fall and winter diet will include weed seeds ... and grain, especially corn." Additionally "... when severe climatic conditions prevail they [greater prairie-chickens] appear to deliberately seek the concentrated grain food." Variation in availability of winter food in an agriculture/grassland landscape may result from factors such as

snow cover, crop rotation, and autumn plowing of grain fields. Flocks routinely used the same grain fields for feeding during winter in Wisconsin, but extensive snow cover forced birds to find and use new areas (**Figure 15**; Hamerstrom and Hamerstrom 1949). Similarly, Mohler (1952) observed flocks using sorghum shocks when snow depth reached 25 cm and access to waste corn was reduced.

In some cases, the availability of grains as a winter food source may determine the presence of birds within a local region. Mohler (1963) studied populations in Nebraska and noted that greater prairie-chickens were not found in the areas of Keith County where corn was not grown. When recounting historical numbers of greater prairie-chickens in Nebraska, Kobriger (1965) concluded that greater prairie-chicken populations declined as corn acreage decreased. Svedarsky and Van Amburg (1996) point out that high levels of cultivated grains are found in the diets of greater prairie-chickens in Missouri; however, the north-central states typically experience more severe winter conditions than Missouri, and therefore the availability of grains for winter food in these areas may be especially important.

The proportion of cultivated grains in the diet decreases during the spring and summer (**Table 4**) as birds increasingly forage on native vegetation, especially forbs (Rumble et al. 1988). The proportion of insects in the summer diet of adult birds varies among different studies: 42 percent in North Dakota (Rumble et al. 1988), 29 percent in Texas (Lehmann 1941), 4 percent in Missouri (Toney 1980), and less than 1 percent in Missouri (Korschgen 1962). This variation may reflect differences in annual insect abundance and/or regional habitat quality.

Table 6. Major categories of diet items for greater prairie-chickens (modified from Svedarsky and Van Amburg (1999).

Food item(s)	Autumn (Sep-Nov)			Winter (Dec-Feb)		
	a	b	c	a	b	c
Cultivated grains	60.7	52.7	33.5	70.8	56.6	56.3
Native vegetation	28.6	29.4	22.0	9.3	10.0	43.5
Misc. Plant material	4.3	12.6	24.8	8.9	0.0	0.0
Green grass	3.6	0.0	9.4	7.0	3.8	0.0
<i>Rosa</i> spp.	1.5	0.9	9.0	2.6	29.4	0.0
Insects	0.0	0.3	1.1	0.0	Trace	0.0

^aKorschgen (1962): Missouri - fecal droppings.

^bBaker (1953): Kansas - crop contents.

^cToney (1980): Missouri - fecal droppings.

^dRumble et al. (1988): North Dakota - fecal droppings.



Figure 15. The availability of winter food is often determined by the weather conditions, such as in this field in northeastern Colorado. Photograph by Michael A. Schroeder.

Insects comprise the majority of food items eaten by chicks (**Table 5**); similar findings have been reported for greater sage-grouse (Schroeder et al. 1999), lesser prairie-chickens (Giesen 1998), and sharp-tailed grouse (Connelly et al. 1998). During the first month of life, up to 98 percent of the diet may be insects, with grasshoppers and beetles the most common foods eaten (Jones 1963). Little information exists regarding daily food requirements; however captive-reared Attwater's prairie-chickens consume an average of 16.2 g of grasshoppers per day (Griffin et al. 1997). The most critical time for the young of most grouse is the first 20 days after hatch when chicks have a rapid growth rate and develop thermoregulatory ability (Dobson et al. 1988). For instance, newly hatched, captive-reared sharp-tailed grouse chicks weigh on average 12.8 g ($n = 138$), and by 100 days following hatch, male and female chicks exceed 700 g and 600 g, respectively (McEwen et al. 1969). Consumption of insects by sharp-tailed grouse chicks accounted for 92 percent of their diet during the first three weeks of age, 63 percent at seven weeks, and 9 percent at 12 weeks of age (Kobriger 1965). Captive greater sage-grouse chicks required insects in their diet for survival, especially during the first three weeks of age. For older chicks, survival and

growth rates increased as the proportion of insects in their diet increased (Johnson and Boyce 1990). Griffin et al. (1997) concluded that recent declines of Attwater's prairie-chickens may reflect inadequate insect biomass to support chick growth due to the combined effects of cattle egrets (*Bubulcus ibis*), fire ant (Myrmicinae) infestations, and use of insecticides.

Diet and behavior

Little information exists regarding the foraging behavior, daily intake, and nutritional requirements of greater prairie-chicken chicks. Anecdotal accounts suggest that greater prairie-chickens, primarily females, seasonally moved extensive distances to wintering areas that provided suitable food and cover (Schmidt 1936). The introduction of corn as a food resource may have led to a reduction in the frequency and extent of these seasonal movements (Gross 1930, Leopold 1931). Schroeder and Braun (1993) monitored 82 radio-marked greater prairie-chickens and concluded that regional food availability did not explain the observed seasonal movements of birds. Most movements were in mid-summer; movement direction was random; extensive overlap occurred with some birds moving

into areas vacated by others; some individuals remained in the same area year-round; and corn was available throughout the region during the year.

Food abundance and distribution

Grain crops, forbs, and insects are major food items of greater prairie-chickens in Region 2 (**Table 4**, **Table 5**, and **Table 6**). Availability of grain crops is largely determined by agriculture practices (e.g., crop rotation, tilling, harvest) and policies (e.g., CRP), and it may vary both annually and regionally. Forb diversity and abundance on rangeland are primarily influenced by grazing practices (Fuhlendorf and Engle 2001) but may also be affected by burning, mowing, spraying, and weather. Insects are important diet items for greater prairie-chicken chicks. Although insect abundance has been found to be highest in habitats with a high proportion of forbs (Jones 1963), relatively little is known regarding insect/plant associations important to greater prairie-chickens. Insect availability may be influenced by factors that alter vegetation composition (e.g., grazing, herbicide spraying), weather, and pesticide spraying.

Breeding biology

Breeding behavior

Greater prairie-chickens are one of several species of Tetraoninae that have a lek mating system, which has the following characteristics:

- ❖ males provide no parental care
- ❖ females come to an arena or lek (where most males aggregate) for mating
- ❖ display sites used by males do not contain specific resources required by females, except the males themselves
- ❖ a female can choose a mate once she visits the lek (Bradbury 1981).

Lekking species typically exhibit elaborate courtship behaviors and displays (Bradbury 1981, Höglund and Alatalo 1995).

The primary display performed by male greater prairie-chickens during the lekking period in spring is referred to as “booming”. Several behaviors are performed to produce the booming display; males extend their eye combs, lower their head, erect pinnae feathers

on their neck, point their tail somewhat forward, stamp their feet on the ground, click their tail, stiffen, shake, and drop their wings until the tips of the primaries touch the ground, expand their esophageal air sacs, and produce a booming vocalization (Lehmann 1941, Hamerstrom and Hamerstrom 1960, Hjorth 1970). This vocalization is relatively low in frequency and is similar to the sound produced when air is blown across the top of a bottle (Hamerstrom and Hamerstrom 1960, Sparling 1983); phonetically it can be described as *whhooo-doo-dooooohh* (Gross 1930). The booming display functions in both territory defense and courtship, and when performed collectively, it also advertises the presence of a lek to females in the vicinity. In addition to the booming display, males perform a “flutter jump” where they leap into the air while flapping their wings, often producing whoop, cackle, or whine calls (Hamerstrom and Hamerstrom 1960, Robel 1964, Hjorth 1970). Flutter jumps, and whooping and cackling vocalizations tend to increase in frequency when females are near or visiting the lek (Hamerstrom and Hamerstrom 1960; Robel 1964, 1967; Sparling 1981).

Male greater prairie-chickens generally display on leks (traditionally referred to as booming grounds) from early March to June, with peak display activity occurring from April to mid-May (Robel 1966, Westemeier 1971, Hamerstrom and Hamerstrom 1973). An autumn display is common, but male attendance is less regular and the display tends to be less intense (Hamerstrom and Hamerstrom 1955). Factors such as weather, season, and temperature may influence male attendance and/or display activity at the lek (Robel 1964). During years of mild weather, males have been noted to periodically display on leks throughout the winter (Baker 1953). In the spring, males usually display for two to four hours at dawn and dusk, with the most intense activity occurring approximately 45 minutes prior to sunrise and when females are visiting the lek (Hamerstrom and Hamerstrom 1955, 1973). During calm conditions, displaying males may be heard by a human observer from a distance of greater than 3 km (Hamerstrom and Hamerstrom 1973). Because leks, and hence individuals, can be located during the spring display period, surveys for greater prairie-chickens are typically conducted at this time.

Male greater prairie-chickens establish territories on lek sites that they actively defend against other males. These territories consist of a core area, where neighboring males are seldom encountered, and peripheral or boundary areas, where aggressive encounters with other males occur (Robel 1966). The area of the territory varies with the dominance rank of

the male; for example, Robel (1967) found that males responsible for most of the copulations at a lek (68 to 74 percent) also held the largest territories (mean = 915 m², $n = 3$, vs. mean = 503 m² for all males, $n = 15$). As well, territories of dominant males are commonly centrally located in relation to territories of other males at the lek (Hamerstrom and Hamerstrom 1973). Territory boundaries often follow natural features of the landscape such as furrows, drainages, swales, grass tussocks, and cow droppings, but many times they have no discernible landscape feature (Hamerstrom and Hamerstrom 1960). Regard for territory boundaries is somewhat flexible as males will commonly move out of their territory to follow a female as she walks through the lek. Hamerstrom and Hamerstrom (1960:279) likened the effect of a female walking through a lek to “a spoon drawn slowly through a plate of thick soup”.

The number of males observed at leks fluctuates early in the spring; by the peak of the breeding season the number of males attending a lek tends to be relatively stable, then it tapers off as female visitation declines (Robel 1967, Schroeder and Braun 1992b). In contrast, the number of males remained relatively stable throughout the breeding season at leks in Wisconsin (Hamerstrom and Hamerstrom 1973).

The peak of female attendance on leks varies regionally; peaks occur between late March and early April in Kansas (Robel and Ballard 1974), in mid-April in Minnesota (Svedarsky 1988), in early April in Colorado (Schroeder and Braun 1992b), and during the third or early fourth week of April in Wisconsin (Hamerstrom and Hamerstrom 1973). The peak in female attendance precedes (on average 3 days), or is coincident with, the peak in mating activity (Hamerstrom and Hamerstrom 1973). During the peak of mating activity, females often visit leks in small flocks of three to six birds. Social dominance interactions have been observed within these flocks whereby the socially-dominant female prevents subordinates from mating until she has mated or left the lek (Robel and Ballard 1974). A second peak in female attendance occurs approximately two to three weeks after the initial peak, when unsuccessful or possibly late-nesting females return to the lek to remate; lek attendance by females is more sporadic at this time (Hamerstrom and Hamerstrom 1973, Svedarsky 1988).

Breeding site fidelity

Lek sites are considered to be traditional as they are often used by birds year after year. Although many lek sites are “permanent” (stable), several “temporary” (unstable) leks may be located within a region during

the breeding season. In eastern Colorado, Schroeder and Braun (1992b) examined 80 lek sites during a 6-year period; 20 leks (25 percent) were active all six years while 26 (33 percent) were active for only one year. The presence of temporary leks may reflect annual population fluctuations, becoming more common when the population increases (Hamerstrom and Hamerstrom 1973, Schroeder and Braun 1992b). Additionally, temporary leks tend to occur early in the spring and may not be active during the peak of the breeding period (Westemeier 1971). Attendance by males on temporary leks tends to be relatively low compared to attendance on permanent leks. In a long-term study in Wisconsin, Hamerstrom and Hamerstrom (1973) found less than 10 percent of temporary leks (defined as those with uncertain status) ever exceeded five males. Similarly, a positive correlation between lek stability and lek attendance was observed by Schroeder and Braun (1992b) in a 6-year study of radio-marked birds; 10.8 males on average visited leks active six years versus only 3.6 males at leks active one year.

The relocation of some males to different leks, and movements by yearling males in an attempt to establish breeding territories, create a dynamic situation in early spring with respect to lek attendance. Once males establish a breeding territory on a lek, they usually remain faithful to that site in subsequent years. Hamerstrom and Hamerstrom (1949) followed 21 individually marked males for several years, 15 (71 percent) consistently returned to the same lek each breeding season while three birds relocated after one year and three birds after two years. Likewise, Schroeder and Braun (1992b) recorded use of the same lek site in consecutive years by six radio-marked and 10 individually banded males. Yearling males have been observed on as many as six different leks in a single breeding season, and occasionally on two different leks during the same morning (Bowman and Robel 1977, Schroeder and Braun 1992b). When dominant males are removed from a lek, vacant territories are rapidly filled by previously non-territorial birds (Robel and Ballard 1974). During the normal display period, males usually visit a lek (94 percent of observations for 13 radio-marked males) and commonly feed and/or loaf nearby during the day, and roost there at night (Schroeder and Braun 1992b). However, single territorial males are occasionally observed displaying daily at a site removed from an established lek (Hamerstrom and Hamerstrom 1973, Schroeder and Braun 1992b).

Although lek sites become inactive as populations decline, variation in lek stability among years also reflects the relocation of leks in response to such factors

as localized habitat change (Yeatter 1943, Anderson 1969). For instance, Schroeder and Braun (1992b) working in Colorado noted the formation of a new lek on a recently disturbed site. The new lek established relatively close to three previous lek sites, one of which had been known to be occupied for at least eight years and one for possibly 70 years (according to anecdotal information). The three “old” leks disappeared (combined number of males decreased from 18 to 0) as lek attendance at the “new” site increased. Similar fluctuations have been noted by Westemeier (1971) in Wisconsin where increases in lek attendance at one lek were coincident with a decline in attendance at a neighboring lek. Additionally, early in the breeding season the specific site of a lek may change several times within a local area before finally becoming established (Westemeier 1971).

While territorial males exhibit high fidelity to a single lek, females commonly visit more than one lek during the breeding season. Schroeder (1991) monitored 79 radio-marked females and observed that 85 percent (67 of 79) visited more than one lek during a breeding season. However, considerable variation exists with respect to female lek visitation; during this study, one female was observed on six different leks (eight visits), and another female visited the same lek on nine consecutive mornings. No differences in lek visitation were detected between adults and yearlings. Females do show fidelity to a nesting area. In Colorado, nest locations between consecutive years averaged 0.8 km apart for eight radio-marked females; this did not differ from the average distance of 0.8 km apart between an individual female’s first and renesting attempts within a year. Females monitored in Minnesota have been found to nest as close as 4.6 m from their nest site the previous year (Svedarsky 1988).

Parental care, brood break-up, and dispersal

Parental care is provided by females while the males play no role in incubating or rearing chicks. Females incubate clutches for 23 to 25 days (Schroeder and Robb 1993), but clutches initiated later in the breeding season may have shorter incubation periods (Svedarsky 1988). Hatching of the clutch may take one to two days, and broods leave the nest within 24 hours following hatch (Lehmann 1941, Svedarsky 1988). The chicks are precocial, cryptically colored, and weigh 11 to 12 g (Schroeder and Robb 1993). When leaving the nest, females travel through lightly vegetated areas with their chicks; the chicks usually stay less than 5 m from the hen. During the first week, the female may brood her chicks as much as 50 percent of the daylight period

as well as spend considerable time in vigilant behavior (Lehmann 1941).

Broods are relatively mobile. In the first 28 hours, broods may travel up to 1.4 km and up to 3.8 km by the first week. By 14 days of age, broods may be located on average 1.0 km from their nest site, and by four weeks of age this distance averages 1.6 km (Svedarsky 1988). Movements of 2 to 11 km have been recorded for broods 34 days of age (Newell et al. 1988). Abrupt movements by broods to new areas may be precipitated by sudden changes in land use (e.g., grazing, mowing) and/or chick predation (Newell et al. 1988). In some cases these movements may be fairly extensive, as far as 11 km. Individual brood ranges (from hatch to brood break-up) are highly variable in overall area, 22 to 2,248 ha (mean = 489, $n = 15$); however, small portions of the brood range are commonly used more intensively (Newell et al. 1988). These smaller areas vary from 9 to 83 ha and may be used for as much as 31 days ($n = 5$ broods, Newell et al. 1988). The overall size of the brood range may be influenced by several factors. Brood range size of first clutches is larger than those of reneest clutches; adult females have smaller brood ranges than yearlings; and mobility of greater prairie-chickens may decline through the summer (Newell et al. 1988).

Many aspects of brood break-up and juvenile dispersal are poorly understood. However, available information suggests that brood break-up and natal dispersal are two separate processes (Bowman and Robel 1977). Brood break-up commences when individuals in a brood become more solitary and scattered, usually during late August and early September. Although brood members move independently, or in pairs, within the brood home range, they commonly roost together at night. The distance between brood members gradually increases through September. Brood break-up may possibly be initiated by environmental factors rather than juvenile age (Bowman and Robel 1977).

Natal dispersal of juvenile greater prairie-chickens is possibly influenced by factors such as age, photoperiod, and proximity to flocks (Bowman and Robel 1977). The early phase of dispersal is generally completed in September and October, when birds make short distance movements (approximately 1.1 km per day for five birds over one to four days). Some birds remain on their brood area through early autumn (Bowman and Robel 1977). Females move farther than males between first wintering and breeding areas; 7 percent of 369 juvenile males versus 47 percent of 125 juvenile females moved more than 8 km (Hamerstrom and Hamerstrom 1973). Distances moved can be as far

as 47 km (Hamerstrom and Hamerstrom 1949). Female chicks in Minnesota nested on average 12.3 km ($n = 11$, range 4.8 – 48.2 km) from their natal territory while 14 males all remained within 4.8 km of where they had fledged (Svedarsky and Van Amburg 1996).

There is evidence that in Tetraoninae an individual's migratory movements mirror its initial dispersal movement between its first wintering and breeding areas (see discussion in Schroeder and Braun 1993). Migratory movements by female greater prairie-chickens are longer and more variable than those of males. For greater prairie-chickens monitored in Colorado, females moved an average of 9 km (range <1 – 40 km), and males moved an average of 2.7 km (range 1 – 6 km) between winter and breeding areas. Distances moved tended to be greater for yearlings than for adult birds for both males (3.5 versus 2.3 km) and females (14.4 versus 8.2 km) (Schroeder and Braun 1993).

Demography

Genetic characteristics and concerns

A population is generally defined as the individuals of a specific species in a particular group, or in a particular area. In most instances, a population is an assemblage of groups distributed over a large area (Soulé 1987). Fundamental to population genetics is the fact that small or isolated populations (with few individuals and no immigration) lose genetic variation over time, thereby increasing the probability of extinction and decreasing the probability of future adaptive change (Lande and Barrowclough 1987). The genetic structure of a population is determined by mutation, random genetic drift, natural selection, and gene flow; as gene flow is decreased, genetic variation is lost due to random genetic drift (Ewens et al. 1987, Slatkin 1987). Genetic variation is believed to be important for a population's long-term persistence because it prevents the deleterious effects of inbreeding and the random loss of alleles through genetic drift. The amount of genetic variation in a population is in part a function of what is termed effective population size, or the "... number of individuals in an ideal population that would have the same genetic properties (in terms of random genetic drift) as an actual population with its own complicated pattern of demographics, sex ratio, etc." (Lande and Barrowclough 1987:99). For greater prairie-chickens, which have a lek mating system (an estimated 10 percent of the male population breeds in any given year [Robel 1970]) and limited dispersal, calculations of effective population size may

underestimate the ideal population needed to maintain genetic diversity (Bouzat et al. 1997).

The broad-scale loss and fragmentation of the historical range of greater prairie-chickens have isolated some populations and/or reduced or eliminated others. In Region 2, the current distribution of greater prairie-chickens consists of core areas connected by smaller, more localized, populations. Viability of these small populations may be maintained by immigration of individuals from larger populations in core areas. However, current trends indicate declining populations in the Flint Hills (Kansas) and the Sandhills (Nebraska), the two largest strongholds for greater prairie-chickens in these states. Dispersal of individuals from the core areas to peripheral populations may be adversely affected by such declines, increasing the likelihood of extinction in peripheral populations and further isolation of core areas.

Recent genetic studies of greater prairie-chickens in Illinois highlight the importance of genetic variation in management considerations. The Illinois population of greater prairie-chickens declined from an estimated several million birds distributed over 60 percent of the state during the mid-1800s, to an estimated 2,000 individuals in 179 sub-populations by 1962, and finally to a low of 46 individuals in two populations by 1994 (**Figure 2**). The decline in greater prairie-chickens between 1962 and 1994 occurred despite intensive management efforts to improve habitat, control nest parasites (ring-necked pheasants), and control predators (Westemeier et al. 1998). Declines in reproductive parameters such as egg fertility (fertile incubated eggs per total eggs) and hatching rate (hatched eggs per total eggs in fully incubated clutches) were associated with contraction and decline of the population (Westemeier et al. 1998), and genetic studies indicated significantly lower levels of genetic diversity in the Illinois population than in larger, more continuous populations (Bouzat et al. 1997). A subsequent translocation of greater prairie-chickens from Minnesota, Kansas, and Nebraska resulted in significant increases in egg fertility and hatching rates in the Illinois population. Westemeier et al. (1998) concluded that the Illinois population would have inevitably gone extinct without this intervention, as it would have been unable to recover the genetic variation necessary to offset environmental effects. It is interesting to note that the 1962 population of 2,000 greater prairie-chickens in Illinois exceeded the current populations in Minnesota, Wisconsin, Missouri, North Dakota, Oklahoma, and Iowa. Similar declines in greater prairie-chicken populations have been observed

in other parts of their range, with different outcomes. In the Sheyenne National Grassland of North Dakota annual counts of breeding males ranged from three to nine during the 1960s and early 1970s. By 1980 the total count of males had increased to 410 birds but declined again to 69 males by 1997 (Kobriger et al. 1988, Kobriger 1999). Greater prairie-chickens in Colorado numbered approximately 600 individuals in 1973; however, the population increased to over 6,000 birds by 1985 and continued to increase to between 8,000 and 10,000 birds by the late 1990s (Giesen and Schroeder 1999).

Hybrids between greater prairie-chickens and sharp-tailed grouse have been found where populations are sympatric (Gross 1930, Ammann 1957). Both species have similar breeding phenologies, but in most instances recognition of conspecific displays and spacing mechanisms are believed to reduce the frequency of hybridization (Sparling 1980). Hybridization tends to occur in areas where one species is more abundant than the other, and females of the less abundant species are believed to have difficulty locating conspecifics, which results in interspecific matings (Ammann 1957, Sparling 1980). The one published account of a sharp-tailed grouse female copulating with a greater prairie-chicken male occurred in an area where greater prairie-chickens outnumbered sharp-tailed grouse (Svedarsky and Kalahar 1980). Hybrids are at least partially fertile (Sparling 1980), and it has been suggested that in areas where the two species overlap, sharp-tailed grouse will eventually replace greater prairie-chickens. F1 females may show a preference for sharp-tailed males, and sharp-tailed grouse are known to dominate greater prairie-chickens during social encounters (Kobriger 1965, Sparling 1981, Toepfer 1988, Toepfer et al. 1990). However in some cases, male greater prairie-chickens on a lek have been known to band together and attack intruding male sharp-tailed grouse. Observations of mixed leks on the Sheyenne National Grassland suggest that even though sharp-tailed grouse display on greater prairie-chicken leks, they do not hold a dominant territory (Schmidt 1980).

Life history characteristics

Although yearling males (0.5 to 1.5 years of age) are physiologically capable of breeding, adult males on leks apparently do most of the breeding (Robel 1964). All females are believed to breed the first year following hatch (Schroeder and Robb 1993) and usually lay one completed clutch per season, but they may lay a renest clutch following failure of the first nest (Svedarsky 1988). Although most adult females

are able to renest, some yearling females apparently do not (Svedarsky and Van Amburg 1996). The average clutch size for greater prairie-chickens is 11 to 12 eggs (range 5 to 17; Schroeder and Robb 1993, Peterson and Silvy 1995). Clutch size of a female's first nest of the season is greater than the clutches of subsequent renests (Hamerstrom 1939, Robel 1970, Drobney and Sparrowe 1977, Svedarsky 1988). In Colorado, clutch size of first nests averaged 12.6 eggs, and renests averaged 9.7 eggs (Schroeder and Robb 1993). Females are more likely to renest if nest loss occurs during laying or early to mid incubation; they are capable of laying at least two renests in a season (three clutches per season) (Svedarsky 1988).

Hatching success of eggs averages 94 percent (range 80 to 100 percent, $n = 216$ successful clutches; summary of 18 studies, Westemeier et al. 1998). Fertility of eggs averages 86 to 98 percent (Gross 1930, Lehmann 1941, Grange 1948, Svedarsky 1988) but may be as low as 74 percent in small declining populations (Westemeier et al. 1998). Svedarsky (1988) found infertile eggs in six of 19 nests, with a mean of 3.3 (range 1 to 6) infertile eggs per nest. Occasionally total clutches are infertile (Yeatter 1943).

Nest success (proportion of nests that hatch at least one egg) averaged 44 percent in Colorado (Schroeder and Robb 1993), 65 percent in Minnesota (20 of 31 nests hatched; Svedarsky 1988), and 26 percent in Kansas (five of 19 nests hatched; Robel 1970). Average nest success was estimated at 49 percent for 934 nests from 22 studies of greater prairie-chickens in North America (Bergerud 1988b). Annual variation in nest success may occur because of differences in weather, age structure of nesting females, and predation rates. Because unsuccessful females may renest following failure of their first nest, annual reproductive success for females tends to be higher than nest success; 48 percent of 69 females produced a brood in Colorado (Schroeder and Robb 1993) and 49 percent of 45 females produced a brood in North Dakota (Newell et al. 1988).

Svedarsky (1988) reported only one of 11 broods survived to the end of August, and this brood had only two chicks; of 116 chicks that hatched, only two survived longer than six weeks. Newell et al. (1988) had 59 percent of 22 broods alive at the end of summer; 28 percent of 261 chicks that hatched survived to 31 August. The estimated number of chicks per brood, prior to brood breakup, averages 6.0 birds (Peterson and Silvy 1996, estimate is weighted mean and based on studies from eight states).

The average lifespan for a greater prairie-chicken is 1.6 years (Robel and Ballard 1974). Annual survival estimates are based on a hunted population in Wisconsin; annual survival rate is approximately 48 percent for yearling males, 45 percent for adult males, 41 percent for yearling females, and 49 percent for adult females (Hamerstrom and Hamerstrom 1973). The knowledge as to which demographic components (life stages) exert the greatest effect on population growth is important. We adapted a population model (Caswell 2001) to evaluate the finite rate of population change (λ) for a generalized population of greater prairie-chickens based on average estimates from throughout the range (**Figure 16, Table 7**). The rate of growth for this population was estimated to be 0.687. This value was extremely low and was well below the 1.0 rate necessary for a stable population. Although it is not clear why this growth rate was so low, substitution of alternate parameter estimates had a dramatic effect on the estimated growth rate. For example, replacement of 15 percent (Svedarsky 1988) with 55 percent (Baker 1953) as the survival rate of

chicks from hatch to about 40 days of age increased the estimate of λ to 1.329.

Sensitivity analysis has been used to address these questions by determining the effect of various life history stages on λ (Caswell 2001). Sensitivity analysis of vital rates for greater prairie-chickens indicates that the combination of nest success and brood survival has the greatest effect on population growth (Wisdom and Mills 1997). For example, an increase of chick survival from 15 percent to 34.5 percent was needed to increase λ from 0.687 to 1.000. Unfortunately, chick survival is also the most difficult parameter to estimate accurately.

Population regulation

Intrinsic factors (i.e., spacing behavior) have been suggested to influence survival and reproduction in various grouse species (Hannon 1988). Greater prairie-chickens are highly social throughout the year; even during the breeding season, males form flocks

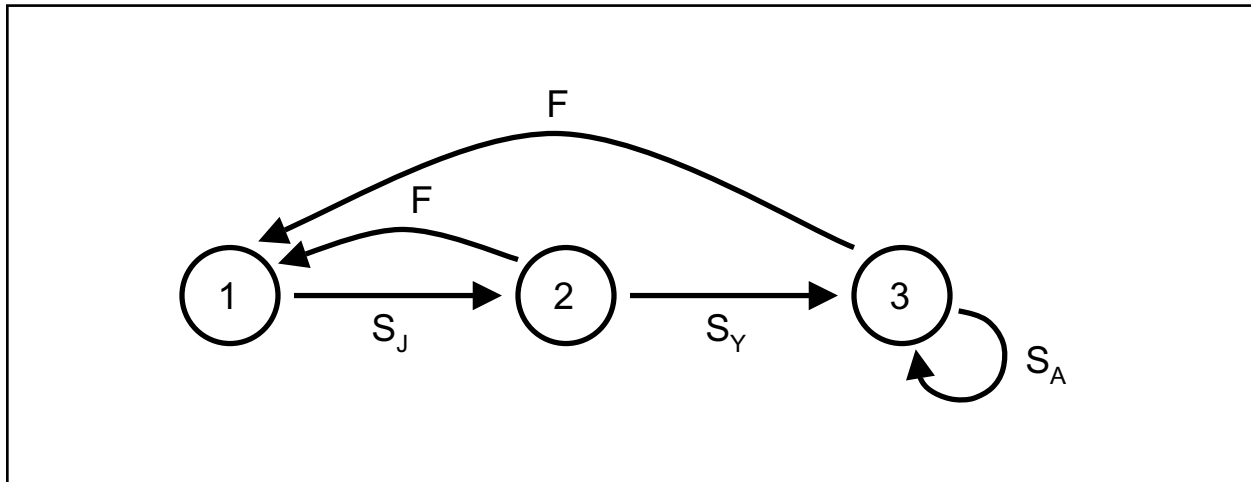


Figure 16. Life cycle diagram for the greater prairie-chicken (based on techniques in Caswell 2001). Data for the parameters are provided in Table 7.

Table 7. Parameter values for productivity and survival for female greater prairie-chickens (Baker 1953, Svedarsky 1988, Schroeder and Braun 1991, Schroeder and Robb 1993, Wisdom and Mills 1997).

Parameter	Estimate	Label used in Figure 16
Average number of female fledglings produced ^a	0.45 fledglings	F
Survival of juveniles from fledging to the next spring	54%	S_J
Annual survival of yearlings	41%	S_Y
Annual survival of adults	49%	S_A

^aThe average number of female fledglings produced combines nesting and renesting likelihood (100 percent for first nests, 17 percent for renests), success (44 percent for both), and clutch size (12.6 eggs for first nests, 9.7 eggs for renests), as well as chick survival through about 40 days of age (15 percent).

with other males from the same lek, and females often visit leks in small groups (Schroeder and Robb 1993). Robel (1970) suggested that mortality of non-territorial males might be higher than that of more aggressive territorial birds. Aggressive behavior by dominant females on leks may result in two to three day delays in mating of subordinate females or in interruptions of copulations (Robel 1970, Hamerstrom and Hamerstrom 1973, Robel and Ballard 1974). Robel (1970) suggested that delays in mating, and hence nest initiation, might reduce productivity of the population as nest loss was higher for nests initiated later in the season in his study. Schroeder and Braun (1992a), however, found no difference in nest success between first nesting (median date of initiation May 10) and renesting (median date of initiation May 25) attempts in Colorado. However, if delayed mating results in a later date of nest initiation, then an individual female's fitness may be affected as there would be less time available to renest. This type of behavior has been considered to have significant impacts on populations in other species of grouse (Hannon 1988). However, the importance of this type of behavior on greater prairie-chicken demography is unknown.

Extrinsic factors (i.e., weather, predation, habitat, disease) have also been suggested to influence survival and reproduction in various grouse species (Angelstam 1988); however, the relative importance of the various factors and how they interact is often unclear (Boag and Schroeder 1992, Zwickel 1992, Braun et al. 1993, Flanders-Wanner et al. 2004). Habitat that provides adequate cover for nesting and brood rearing is believed to be limiting for greater prairie-chickens throughout their range (Westemeier and Gough 1999). Habitat degradation caused by heavy grazing, annual burning, and invasion of woody vegetation may adversely affect nest success as dense cover is believed to provide greater concealment of nests from predators for most species of grouse (Bergerud 1988a, b). This was found true for Attwater's prairie-chickens where visual obstruction was higher at successful than unsuccessful nest sites (Lutz et al. 1994). The degree of openness of the habitat is important as evidence suggests that nest predation is lower in treeless grasslands than in areas interspersed with brushy cover (Svedarsky 1988, McKee et al. 1998). Habitat fragmentation may negatively impact nest success by forcing birds to nest in marginal habitats, by increasing travel time through unsuitable areas, and by increasing the diversity and density of predators (Ryan et al. 1998, Schroeder and Baydack 2001). Long moves may be energetically expensive for young chicks and expose them to a greater risk of predation. Svedarsky (1988) believed that brood movements, as

well as precipitation and temperature, were key factors affecting chick mortality in Minnesota.

During the hatching and post-hatching period, young chicks are susceptible to chilling when conditions are cool and wet. Horak (1985) suggested that weather conditions during spring can affect nest success in Kansas as rainy, cool spells resulted in increased nest destruction and desertion. Similarly, Gross (1930) refers to cold and rainy spells during early June as disastrous for broods in Wisconsin. Svedarsky and Van Amburg (1996) suggested that a significant loss of entire broods may occur within a relatively short time, depending upon chick age, amount and duration of rainfall, and temperature. Weather may also indirectly affect chick survival by influencing insect populations (food base) and vegetative growth (cover). Cool, moist summers are associated with higher productivity of greater prairie-chickens in South Dakota as populations were lowest during 1977, the year following a severe drought (Fredrickson et al. 1999); moisture may be important in South Dakota for increasing vegetative growth and hence cover for chicks. Svedarsky (1988) recorded a 25 percent increase of males on leks the year following the second-driest on record in Minnesota and suggested that increased numbers of birds reflected high productivity the previous year due to favorable conditions. These observations have also been noted with sharp-tailed grouse (Flanders-Wanner et al. 2004).

Predation can be a significant mortality factor for nesting females (Schroeder and Robb 1993). Svedarsky (1988) estimated a 57 percent (10 of 21 females were predated) mortality rate for females during summer (May - August). He equated this to an annual mortality rate of 228 percent (if the monthly summer mortality rate of 19 percent were constant throughout the year). Newell et al. (1988) had 21 of 44 (48 percent) females die between April and August. Many species of hawks, owls, and mammals are known predators of chicks and mortality is high especially during the first couple of weeks following hatch (Schroeder and Robb 1993). Newell et al. (1988) determined that chick mortality averaged 63 percent ($n = 22$ broods, 261 chicks) during the first 24 days following hatch while mortality later in the summer averaged 9 percent. Horak (1985) estimated a loss of three chicks per brood (249 broods) during the first three weeks following hatch but was not able to determine the exact cause of mortality. Interactions with exotic species also may indirectly impact brood survival. For instance, in parts of the Attwater's prairie-chicken's range that have been infested with fire ants insect numbers have decreased by as much as 75 percent. Insect numbers are believed to be insufficient

to support broods in these areas, resulting in low chick survival (Griffin et al. 1997).

Similar to other grouse species found worldwide, the most common threats to greater prairie-chicken populations are habitat loss, fragmentation, and degradation and the interaction of these processes to create increasingly isolated populations that are more susceptible to declines in genetic diversity and fertility, and vulnerable to extinction through stochastic events (Westemeier et al. 1999, Bouzat et al. 1997, Storch 2000). Although in many parts of the range a mixture of cropland and grassland is desirable, widespread conversion of habitat to agriculture or development has had potentially detrimental consequences to nesting and brood-rearing areas. Nest and brood success are both critical for population viability and persistence (Wisdom and Mills 1997). In fragmented habitats, nest loss for greater prairie-chickens may be higher than in larger more continuous tracts, as has been observed for other species of ground nesting birds in grassland areas (Johnson and Temple 1990).

In all habitats, degradation of nesting and brooding areas is caused by heavy grazing, mowing, alteration of fire regimes, invasion by woody growth and noxious weeds, and application of herbicides and pesticides (Storch 2000). As much as 90 percent of the tallgrass prairie in the Flint Hills of Kansas is annually burned in the early spring. This practice, followed by intensive grazing, substantially reduces or eliminates nesting and brood-rearing cover for greater prairie-chickens and is believed to be linked to marked regional declines in greater prairie-chicken populations in recent years (Applegate and Horak 1999, Horton and Wolfe 1999). Current status reports from each state in the geographic distribution of greater prairie-chickens emphasize that quantity and quality of nesting and brood habitats are inadequate throughout most of greater prairie-chicken range (Anderson and Toepfer 1999 – Wisconsin, Applegate and Horak 1999 – Kansas, Fredrickson et al. 1999 – South Dakota, Giesen and Schroeder 1999 – Colorado, Kobriger 1999 – North Dakota, Mechlin et al. 1999 – Missouri, Svedarsky et al. 1999 – Minnesota, Vodehnal 1999 – Nebraska, Westemeier et al. 1999 – Illinois). As well, dispersal rates in declining populations may be inadequate for maintaining population connectivity (Johnson et al. 2004).

Community ecology

Predation

Numerous avian and mammalian species are known predators of greater prairie-chickens and their nests (Schroeder and Robb 1993). Primary predators of adult and juvenile birds include red-tailed hawks (*Buteo jamaicensis*), northern goshawks (*Accipiter gentilis*), rough-legged hawks (*B. lagopus*), broad-winged hawks (*B. platypterus*), northern harriers (*Circus cyaneus*), great horned owls (*Bubo virginianus*), and coyotes (*Canis latrans*). Major nest predators include ground squirrels (*Spermophilus* spp.), badgers (*Taxidea taxus*), striped skunks (*Mephitis mephitis*), opossums (*Didelphis virginianus*), raccoons (*Procyon lotor*), coyotes, American crows (*Corvus brachyrhynchos*), and fire ants (*Solenopsis* spp.) (Schroeder and Baydack 2001). Intensity of predation pressure varies and is believed to be linked to changes in predator foraging strategies during population cycles of primary prey items (Schroeder and Baydack 2001). During years of scarce prey, predators may search more intensively and consequently increase their probability of encountering grouse nests (Angelstam 1983). There is evidence that predation levels in grouse populations are also influenced by habitat fragmentation and degradation. Movements by greater prairie-chickens between suitable habitats, such as between feeding and roosting areas, may be further and more frequent in fragmented habitats, thus exposing individuals to higher risk of predation. Fragmentation of nesting habitat may subject females to increased levels of predation (Ryan et al. 1998) as density and diversity of predators may be higher in these areas (Schroeder and Baydack 2001). Fragmentation favors generalist predators, like coyotes and skunks, that have successfully adapted to both agricultural and urbanized landscapes. Modification of grassland habitats by power poles, fence lines, tree plantings, etc. may increase predation levels by creating favorable hunting perches and nest sites for many raptor species, and establishment of livestock watering sites may alter the local distribution of some mammalian predators in drier habitats.

Competition

The historical distributions of lesser prairie-chickens and greater prairie-chickens were

geographically continuous but not overlapping (Aldrich 1963). Greater prairie-chickens generally were found in mid-tall grass prairie while lesser prairie-chickens occupied xeric grasslands with a shrub component of shinnery oak or sand sagebrush. Jones (1963) believed that these habitat differences were great enough to serve as an isolating mechanism between the two species. However, in recent years a sympatric distribution of greater and lesser prairie-chickens has been recorded in west-central Kansas as a result of range expansion by both species, and mixed leks are increasingly common (U.S. Fish and Wildlife Service 2002). How the sympatric occupation of habitat influences use of resources by either species has not been established.

The distributions of sharp-tailed grouse and ring-necked pheasants overlap that of greater prairie-chickens. Both species have been observed at greater prairie-chicken leks and are generally dominant in interspecific encounters (Schroeder and Robb 1993). Whether or not either of these species directly competes for resources is not clear. Sharp-tailed grouse tend to be associated with shrubbier habitats than those used by greater prairie-chickens, especially during winter (Connelly et al. 1998). Aggressive interactions between sharp-tailed grouse and greater prairie-chickens have been observed at common feeding sites; whether greater prairie-chickens are denied access to resources is unknown (Schroeder and Robb 1993, Connelly et al. 1998). Ammann (1957:105) reports "...once sharptails become more abundant than greater prairie-chickens, the latter usually diminish in number very rapidly." Toepfer et al. (1990) mention 12 isolated populations that originally contained both species but experienced a population shift in favor of sharp-tailed grouse. Male ring-necked pheasants are known to harass male greater prairie-chickens at lek sites, and in 78 percent of these interactions pheasants were dominant over greater prairie-chickens (Vance and Westemeier 1979).

Nest parasitism by ring-necked pheasants is known to occur in parts of the range where the species are sympatric. Parasitism rate in Illinois was 3 percent (17 of 497 nests), and parasitized nests were less successful than non-parasitized nests (Vance and Westemeier 1979). The average incubation period for ring-necked pheasants is 23 days, approximately two days less than that required for greater prairie-chickens. Parasitized nests are known to result in failure of greater prairie-chicken clutches as females will leave the nest with pheasant chicks before their own eggs hatch (Vance and Westemeier 1979). Reduced availability of nesting habitats in Illinois may have concentrated greater prairie-chickens and ring-necked pheasants in

a small area, thus increasing the probability of nest parasitism. This observation suggests that the relative importance of nest parasitism may be greater for small populations in fragmented habitats.

Parasites and disease

Parasites of greater prairie-chickens, intensity of parasite infections, and the impact of parasites and disease agents on populations are poorly understood (Peterson 2004). A summary of reported parasites and disease agents suggests that they are common throughout the range (**Table 8**). Although parasites are known to cause significant mortality in some grouse species, such as red grouse (*Lagopus lagopus scoticus*) in Scotland (Hudson 1992), there is little documentation of similar patterns in greater prairie-chickens (Peterson 2004). Nevertheless, caution should be exercised before dismissing the potential for population-level impacts. For example, West Nile virus has had dramatic impacts on some populations of greater sage-grouse (Naugle et al. 2004). Consequently, its potential impacts on greater prairie-chickens should be considered. Ring-necked pheasants can carry *Heterakis gallinarum* with few effects whereas grey partridge (*Perdix perdix*) are likely to die (Tompkins et al. 2000a, b); in areas of pheasant and partridge overlap, the partridge populations may be reduced or eliminated. This type of relationship has not been observed in greater prairie-chickens.

Envirogram

We developed an envirogram (Andrewartha and Birch 1984) to describe the relationship between greater prairie-chickens and their environment (**Figure 17**). This envirogram considers resources (primarily habitat for cover and food), malentities (negative stressors in the environment), and predators. The diagram illustrates the continuum of potential relationships between baseline factors in the environment versus the more proximal causes. These factors are illustrated on a horizontal axis from left to right, or ultimate to proximal, respectively.

This type of relationship can be illustrated for greater prairie-chicken chicks, which depend on insects during their first weeks after hatch. Insect abundance can depend on numerous factors, one of which is plant diversity. Likewise, plant diversity can depend on numerous factors, one of which is the introduction and expansion of noxious weeds in an environment. The prevalence of noxious weeds can be increased by reduced competition from native plant species and/or site disturbance. A site can be disturbed by numerous factors such as the building of a road. Hence, the

Table 8. Reported parasites and disease agents of greater prairie-chickens (modified from Peterson 2004).

Group/Species	State (n positive/total n)	Reference
Cestodes		
<i>Choanotaenia infundibulum</i>	Illinois (2/28)	Leigh 1940
<i>Choanotaenia infundibulum</i>	Wisconsin (2/39)	Morgan and Hamerstrom 1941
<i>Raillietina variabilis</i>	Illinois (10/28)	Leigh 1940
<i>Raillietina variabilis</i>	Wisconsin (1/34)	Gross 1930, Leigh 1941
<i>Rhabdometra nullicollis</i>	Wisconsin (5/39)	Morgan and Hamerstrom 1941
Nematodes		
<i>Trichostrongylus cramae</i>	Texas (8/9)	Peterson et al. 1998
<i>Heterakis gallinarum</i>	Illinois (11/28)	Leigh 1940
<i>Heterakis gallinarum</i>	Kansas (26/106)	Harper et al. 1967
<i>Heterakis gallinarum</i>	Missouri (4/11)	Schwartz 1945
<i>Heterakis gallinarum</i>	Wisconsin (17/34)	Gross 1930
<i>Heterakis gallinarum</i>	Wisconsin (8/39)	Morgan and Hamerstrom 1941
<i>Dispharynx nasuta</i>	Texas (1/3)	Peterson et al. 1998
<i>Dispharynx nasuta</i>	Kansas (14/106)	Harper et al. 1967
<i>Cyrenia colini</i>	Illinois (14/28)	Leigh 1940
<i>Cyrenia colini</i>	Kansas (82/106)	Harper et al. 1967
<i>Cyrenia colini</i>	Missouri (5/11)	Schwartz 1945
<i>Cyrenia colini</i>	Wisconsin (3/34)	Gross 1930
<i>Cyrenia colini</i>	Wisconsin (13/39)	Morgan and Hamerstrom 1941
<i>Capillaria contorta</i>	Wisconsin (6/39)	Morgan and Hamerstrom 1941
<i>Ascaridia galli</i>	Wisconsin	Gross 1930
<i>Ascaridia galli</i>	Wisconsin (2/39)	Morgan and Hamerstrom 1941
<i>Oxyuris petrowi</i>	Michigan	Saunders 1935, Cram 1937
<i>Oxyuris petrowi</i>	Unknown	Addison and Anderson 1969
Other helminthes		
<i>Mediorhynchus papillosus</i>	Illinois (2/28)	Leigh 1940
Ticks		
<i>Haemaphysalis leporispalustris</i>	Wisconsin	Gross 1930
Mites		
Unidentified	Illinois (2/28)	Leigh 1940
<i>Tetraolichus cupido</i>	Texas	Atyeo and Gaud 1992
Mallophaga		
<i>Menopon monstaeum</i>	Illinois (4/28)	Leigh 1940
<i>Menopon</i> sp.	Missouri (2/22)	Schwartz 1945
<i>Lagopoecus perplexus</i>	Missouri (7/22)	Schwartz 1945
<i>Lagopoecus</i> sp.	Oklahoma	Emerson 1951
<i>Chapinia</i> sp.	Wisconsin	Gross 1930
<i>Goniodes cupido</i>	Unknown	Osborn 1896, Kellogg 1899
<i>Goniodes cupido</i>	Nebraska	Emerson 1951
<i>Goniodes cupido</i>	Oklahoma	Emerson 1951
<i>Goniodes cupido</i>	Massachusetts	Gross 1928
<i>Goniodes</i> sp.	North Dakota	Aldous 1943

Table 8 (concluded).

Group/Species	State (n positive/total n)	Reference
Hematozoa		
<i>Plasmodium pedioecetii</i>	Colorado (6/25)	Stabler and Miller 1984
Other protozoa		
<i>Eimeria dispersa</i>	Wisconsin (3/39)	Morgan and Hamerstrom 1941
<i>Histomonas meleagridis</i>	Massachusetts	Gross 1928
<i>Histomonas meleagridis</i>	Wisconsin	Gross 1930
<i>Histomonas meleagridis</i>	Illinois	Leigh 1940
<i>Histomonas meleagridis</i>	Missouri	Schwartz 1945
Bacteria		
<i>Pasteurella multocida</i>	Texas (4/27)	Peterson et al. 1998
Viruses		
Reticuloendotheliosis virus	Captivity	Drew et al. 1998
Reticuloendotheliosis virus	Texas (2/25)	Drew et al. 1998
Reticuloendotheliosis virus	7 states (2/354)	Wiedenfeld et al. 2002

building of a road is one of the root causes (but not the only one) in the loss of insects needed by greater prairie-chicken chicks.

CONSERVATION

Land Management and Its Implications for Greater Prairie-Chicken Conservation

Land use conversion and habitat fragmentation

Land management practices significantly influence the quality and availability of habitat for greater prairie-chickens as this species requires extensive areas of grassland with suitable cover throughout its range (Svedarsky et al. 2000). Conversion of native prairie clearly has had a long-term impact on greater prairie-chickens. According to estimates by Samson et al. (2004), about 70 percent of the Great Plains has been converted, mostly to cropland. There is a tremendous amount of variation in conversion rates by ecoregion (**Table 1**). When condition and patch size of the remaining habitat are factored in, the remaining amount of suitable habitat for greater prairie-chickens is much less than these figures would indicate.

Conversion of habitat within the range of the greater prairie-chicken is not all negative. A cropland/grassland mosaic is an important habitat feature in the northern and western part of this species' range, especially in areas with extended winter snow cover. It is believed that the increase in greater prairie-chicken

numbers during the late 1800s was related to farming practices of the day, whereby small crop fields were interspersed with grasslands creating a favorable mix of food resources and nesting cover (Vodehnal 1999). "At some point, agriculture provided an optimum balance of food and cover for greater prairie-chickens, but they rapidly disappeared once this balance was exceeded" (Applegate and Horak 1999:114).

Small amounts of cropland can be important sources of food for greater prairie-chickens in Region 2, but the relative value of cropland may depend upon the type of crop grown (corn, soybeans, sorghum), its juxtaposition to suitable grassland cover, and farming practices, such as autumn plowing, that influence availability of waste grain. As the proportion of cropland increases, the resulting loss and fragmentation of grassland areas reduce the quantity and quality of habitat for greater prairie-chickens. In Nebraska the primary range for greater prairie-chickens is the Sandhills, especially the eastern and southern edges where grain crops are interspersed with grassland (**Figure 18**). Land use practices in the Sandhills consist of 80 percent rangeland, 10 percent wild hay production, 5 percent cultivated crops, 2 percent woodland, and 1 percent water (Vodehnal 1999). In other parts of Nebraska greater prairie-chickens numbers are lower where more than 30 percent of the habitat is cropland (Vodehnal 1999). Similarly, the tallgrass prairie in the Flint Hills of Kansas is a prime area for greater prairie-chickens because large contiguous tracts of grassland are interspersed with relatively small amounts of cropland, primarily sorghum (Applegate and Horak 1999). The core of greater prairie-chicken

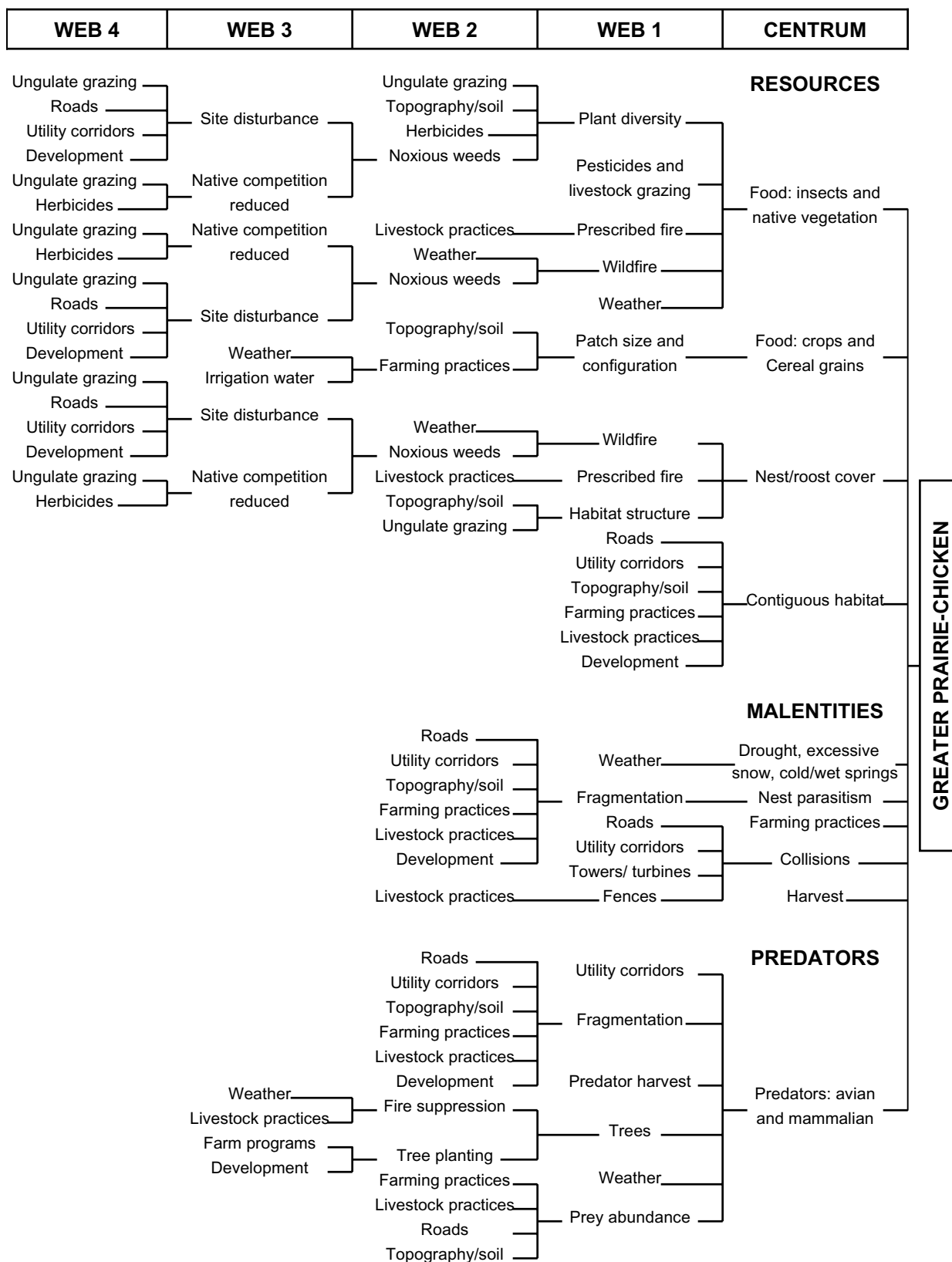


Figure 17. Envirogram for the greater prairie-chicken (based on Andrewartha and Birch 1984).



Figure 18. Greater prairie-chicken habitat in USDA Forest Service Region 2 often consists of grassland configured with croplands, in this case a center-pivot irrigated corn field. Photograph by Michael A. Schroeder.

range in Colorado consists of rangeland (84 percent) interspersed with cropland (13 percent), primarily corn, in a patchwork pattern whereby corn fields are generally located within 3 km of grassland habitat (Schroeder and Braun 1992a).

Fragmentation and isolation of habitat clearly affect greater prairie-chicken populations. The number of males needed in an integrated population for it to be considered viable is somewhat variable, depending on the literature source. Toepfer et al. (1990) suggested that 100 males would be enough to support population persistence over a relatively long period of time. In contrast, the Attwater's prairie-chickens declined rapidly toward extinction, despite having a substantially larger population (Silvy et al. 2004). Closed populations appear to have persisted with fewer than 500 males for 25 years in Minnesota and fewer than 250 males for 50 years in Wisconsin (Westemeier and Gough 1999). However, recent evidence for Wisconsin indicates that populations between 70 and 327 males (1998 data, Anderson and Toepfer 1999) have been insufficient to maintain genetic heterogeneity (Bellinger et al. 2003; Johnson et al. 2003, 2004). This is further supported

with research in Illinois suggesting that declines in both population size and genetic heterogeneity were rapid when the number of males dropped below 200 (Westemeier et al. 1998). These population considerations also can be placed into a spatial context. Winter and Faaborg (1999) found that greater prairie-chickens were absent from prairie fragments less than 77 ha in size in Missouri and that they were one of the most area-sensitive grassland birds studied.

Livestock grazing

Greater prairie-chickens, like other species of grassland birds, evolved with large grazing ungulates such as bison. In recent times, bison have been replaced with cattle and the condition of much of the grassland habitat is now largely determined by land management practices associated with livestock production. As a consequence, management practices for livestock production can significantly impact greater prairie-chicken populations by altering vegetation structure. Greater prairie-chickens are no longer found in areas where livestock management has reduced the quantity of residual herbaceous cover on the rangeland below the

level necessary to support the nesting efforts of females (Svedarsky et al. 2000).

A combination of grazing by ungulates and natural wild fire is believed to have created a patchy distribution of grasslands at differing stages of succession at both the local scale and across landscapes (Fuhlendorf and Engle 2001). Disturbance patterns in the prairie landscape are believed to have resembled a shifting mosaic where recently disturbed patches (by grazing and/or fire) were intermixed with areas undisturbed for several years (Kay 1998, Fuhlendorf and Engle 2001, Samson et al. 2004), creating a heterogeneous landscape at both spatial and temporal scales. Because greater prairie-chickens have relatively small annual home ranges, and nearly all activity is within 5 km of a lek site, this heterogeneity is important on the local scale.

In eastern Kansas, much of the greater prairie-chicken range is burned annually to promote vegetative growth for livestock, in some cases "...entire landscapes horizon to horizon..." (Westemeier and Gough 1999: 176). This practice has likely reduced nesting and brood habitat, especially in portions of the Flint Hills. Conversely, infrequent burning in southeastern Kansas is believed to have allowed encroachment of woody vegetation into the grasslands (Storch 2000). Tree encroachment by eastern red cedar (*Juniperus virginiana*), Osage orange (*Maclura pomifera*), blackjack oak (*Quercus marilandica*), and black locust (*Robinia pseudoacacia*) is a problem in some areas of the Flint Hills and other areas of central and western Kansas where prescribed fires are not part of the normal management strategy (Rodgers et al. 2000).

Suitable nesting habitat is considered a limiting factor for greater prairie-chickens (Kirsch 1974), and nest success and chick survival are believed to be the most important demographic factors influencing their populations (Wisdom and Mills 1997). Residual vegetation is a critical component of nesting habitat. Data collected on the Valentine National Wildlife Refuge in Nebraska between 1956 and 1994 suggest an inverse relationship between AUM (potential intake of forage of one animal unit in one month) utilization and greater prairie-chicken numbers (Svedarsky and Van Amburg 1996 citing unpublished data provided by L. McDaniel). From 1956 to 1976, counts of males on leks averaged less than 60 on less than 10 leks. During this time all meadows were annually mowed for livestock feed, upland areas were grazed following a season-long grazing system, and AUMs averaged greater than 50,000. In 1972 management was initiated to improve nesting cover for greater prairie-chickens. By 1977,

AUMs were decreased to less than 20,000, annual mowing and winter grazing were reduced, a rotational grazing system was implemented, and greater prairie-chicken numbers on the refuge began to increase. However it was not until AUMs were decreased and maintained at less than 10,000 that the population dramatically increased to 401 males counted on 38 leks. The population increase was believed to be related to the presence of significantly more undisturbed cover resulting from reduced grazing pressure and modified grazing practices. Flanders-Wanner et al. (2004) suggested that lower grazing pressure was one reason why productivity for greater prairie-chickens and sharp-tailed grouse was higher on the Valentine National Wildlife Refuge than sharp-tailed grouse productivity was on the McKelvie National Forest, which is also in Nebraska.

Newell et al. (1988) monitored brood movements of greater prairie-chickens in North Dakota and concluded that females with broods tended to avoid pastures with cattle; of 19 brood females, six moved their broods from areas with cattle to areas without cattle, four remained in grazed areas, and nine remained in habitats that had not been grazed that year. However, stocking rates were not given in this study. Drobney and Sparrowe (1977) observed that prairie pastures managed by light to moderate warm season grazing were frequently used by greater prairie-chickens on their study area in Missouri.

Vegetation tends to be denser and taller at successful first nests than unsuccessful nests (Eng et al. 1988, Lutz et al. 1994). First nests have larger clutch sizes than renesting attempts, so they have greater potential to influence annual productivity. Although first nests may be more successful than reneests in some areas (Robel 1970), renesting attempts were more successful than first nests on the Sheyenne National Grassland (Eng et al. 1988). This difference was attributed to reneests having greater cover because of the current season's growth. Direct interactions among livestock and greater prairie-chickens are difficult to observe. However, in a study of artificial nests conducted in grassland habitat in southwestern Wisconsin, approximately 75 percent nest loss was caused by cattle damage (e.g., trampling, crushing by muzzle, eggs kicked out of nest) in all grazing treatments studied (Paine et al. 1996).

Pesticides and herbicides

Pesticide treatment of rangeland and crop production areas may impact greater prairie-chickens, especially chicks, by reducing insect prey and through

direct poisoning as a result of ingestion of pesticides. While no studies have examined the direct effect of chemical spraying activities on greater prairie-chicken populations (U. S. Fish and Wildlife Service 2002), 63 of 200 greater sage-grouse died after feeding in an alfalfa field sprayed with dimethoate (Blus et al. 1989). Application of herbicides may adversely impact nesting, roosting, and brood rearing habitats as has been found for lesser prairie-chickens (Giesen 1998).

Development

Road building (e.g., county roads, highways) can cause habitat fragmentation and degradation by removing potential habitat. Although the area occupied by a roadway may be relatively little, the total impact of a roadway on the surrounding habitat may actually be much greater. In a range-wide conservation assessment of the greater sage-grouse, Interstate 80 in southern Wyoming was found to have a significant impact on the distribution of leks, particularly within 4 km of the interstate (Connelly et al. 2004). This has been noted for other species of birds (Reijnen et al. 1995). Roadways create disturbed sites that are often favorable for incursion and/or spread of noxious weeds, and they may increase the likelihood of wild fires (Connelly et al. 2004). The increased fragmentation associated with roadways may also result in higher diversity and density of potential predators (Connelly et al. 2004). Noise pollution from vehicle traffic, oil/gas drilling operations, and gravel crushing operations may degrade habitat quality for greater prairie-chickens, but a clear cause and effect relationship is difficult to quantify. Moreover, the impacts from noise may be confounded by the loss and fragmentation of habitat that usually accompanies such activities. Urbanization of habitat is a problem where incursions by residential development reduce and/or degrade available habitat. Rodgers et al. (2000) suggest that adverse impacts resulting from ranchette development may be greater than loss of habitat in the immediate area. The accompanying changes in land use practices and the introduction and/or changes in predators may extend the range of influence of urbanized areas.

Transmission towers, wind turbines, power lines, and fences increase the nesting, perching, and roosting sites of raptors, owls, and ravens, and as such they can impact greater prairie-chicken populations by affecting the frequency of mortality by predators. Fatal collisions with towers, turbines, lines, and fences also have been recorded for many species of birds in prairie habitats (Faanes 1987). The range of the greater prairie-chicken is an area being targeted for development by

wind power, due to the relatively high winds (**Figure 19**; Elliott et al. 1987). Greater prairie-chickens also may exhibit a behavioral aversion to anthropogenic structures in their environment, similar to what has been shown with lesser prairie-chickens (Hagen et al. 2004). Hunt (2004) found that factors associated with petroleum development explained approximately 32 percent of the variation between active and inactive lesser prairie-chicken lek sites in New Mexico; leks in petroleum areas were less likely to be active.

Consumptive and non-consumptive recreational use

Recreational hunting of greater prairie-chickens is a long standing tradition in many parts of Region 2. Regulatory mechanisms governing harvest of greater prairie-chickens are determined by individual states, and estimates of harvest are generally determined from data collected via hunter check stations, mail-in wing censuses, wing barrels, and hunter report card surveys (Applegate and Horak 1999, Fredrickson et al. 1999, Vodehnal 1999). Estimated numbers of greater prairie-chickens harvested during 1997 were 16,000 from Kansas and 8,000 for South Dakota; an unknown number was harvested in Nebraska. Greater prairie-chickens are currently hunted in Colorado following several decades of closed seasons. Westemeier and Gough (1999) concluded that hunting was warranted in Nebraska and South Dakota under current regulatory levels but suggested that restrictions may be wise in Kansas where populations have experienced a significant decline in recent years. Fredrickson et al. (1999:78) indicate that annual hunter harvest of sharp-tailed grouse and greater prairie-chickens in South Dakota is approximately 15 to 30 percent of the autumn population. However, the effects of hunting pressure may be proportionally higher for small, isolated populations than ones with greater connectivity as has been suggested for some populations in Kansas (Rodgers et al. 2000).

Recent analysis of patterns of mortality in hunted greater sage-grouse populations revealed adult females have a higher hunting mortality during autumn than adult males (Connelly et al. 2000). Female greater sage-grouse may be more susceptible to hunting mortality than males because of their association with broods and brood behavior; males tend to be more dispersed at this time. In addition, natural mortality may be relatively low during winter (Connelly et al. 2000). In this case hunting may be additive to winter mortality for sage-grouse and essentially reduce the spring breeding populations, especially for females. If a similar pattern of hunting mortality of breeding-age females occurs

for greater prairie-chickens, declining populations and those that are small and isolated may be especially vulnerable to hunting pressure. Hunter harvest of sharp-tailed grouse is known to have variable effects on different populations; harvest rates acceptable in some populations may negatively impact others (Connelly et al. 1998, Giesen 1998).

In some cases, hunting may positively affect greater prairie-chicken populations by creating incentives for habitat preservation and improvement by landowners and hunters. State agencies often use harvest information to evaluate annual productivity of populations. Hunting activity is often viewed by state agencies as a way of generating public interest in a species, and hunters, as a group, often support conservation measures for game species and can be effective lobbyists for their conservation (Storch 2000). In some cases, however, the goals of a state agency with respect to hunting may be at odds with the public perception of conservation. Opinion surveys indicated that hunters and the general public in Colorado supported a hunting season for greater prairie-chickens if populations were large enough, but most landowners in areas inhabited by greater prairie-chickens were not in favor of hunting (Giesen and Schroeder 1999).

In recent years, there has been growing interest from the public to observe greater prairie-chicken courtship behavior during the spring. Several states have responded to this interest by establishing recreational public-viewing blinds near lek sites (Applegate and Horak 1999, Vodehnal 1999). Kansas has initiated a program that allows visitors to record information regarding lek attendance and behavior of greater prairie-chickens at the lek. This information will then be examined to determine if disturbance from the viewing blind and increased human activity near the lek site are adversely affecting the breeding behavior of greater prairie-chickens (Applegate and Horak 1999).

The study of greater prairie-chicken biology and ecological relationships often requires ecologists to closely monitor individual birds and their habitats. As grasslands become fragmented and reduced, fewer areas are available where researchers can study grassland species (both plant and animal) in an intact ecosystem. The Konza Prairie Research Natural Area in Kansas (3487 ha) experienced a 63 percent decline in number of lekking males and a 38 percent decline in number of leks between 1980 and 1990 until by 1999 few greater prairie-chickens were left, though research efforts increased from 26 to 77 projects during the same period (Westemeier and Gough 1999). Simultaneous

declines were not recorded for leks outside the Konza Prairie Preserve boundary. Westemeier and Gough (1999) suggested that this scenario may not be uncommon; low total lek counts (a total of 58 to 126 males) have been recorded on the 15,379 ha Tallgrass Prairie Preserve in Oklahoma concurrent with 43 research projects. Numerous research projects focused on a local population may have the undesired effect of disturbing greater prairie-chickens beyond some tolerance limit. Although a disturbance threshold for greater prairie-chickens is difficult to quantify (different research activities may cause different disturbances), consideration of the cumulative impact of research projects may be important, especially for isolated populations.

Miscellaneous threats

Although grain fields may be beneficial in some areas, farm machinery or related activities may cause nest mortality. In Missouri, 24 percent (5 of 21) of failed nests in a prairie/agriculture mosaic resulted from human-related activities (Ryan et al. 1998). Flooding can cause problems by reducing nesting and roosting cover. The effect of floods largely depends on timing (i.e., a flood prior to or during nesting would potentially limit nesting cover or reduce nest success), frequency, and extent of the area affected. Although there is potential for local flooding in Region 2, most of the direct observations of problems to grouse associated with flooding have occurred in the range of the Attwater's prairie-chicken in southeastern Texas (Silvy et al. 1999). In Texas, an entire population of 20 endangered Attwater's greater prairie-chickens was lost following a major hurricane (Silvy et al. 1999).

Tools and practices

Management approaches

Maintenance of viable populations is a critical component of any management plan. Specific management elements that should be considered include:

- ❖ size of the management area
- ❖ connection of adjacent sub-populations with suitable habitat
- ❖ incorporation of activities associated with livestock production and farming into the overall management scenario

- ❖ recommendations for land use activities that support seasonal and behavioral habitat requirements of greater prairie-chickens
- ❖ consideration of the type and timing of potential disturbances such as off-road vehicles, mineral extraction, wind turbines, and roads
- ❖ recommendations for harvest that consider timing, rate, production, and differential susceptibility by sex
- ❖ consideration of potential obstacles including fences, power lines, towers, and guide wires
- ❖ development of scenarios for intervention, including habitat restoration and population introduction/augmentation
- ❖ consideration of management guidelines that will minimize the negative consequences of habitat degradation and fragmentation, including the increased risk of predation and nest parasitism
- ❖ development of research and adaptive management approaches to address questions pertaining to significant issues such as survey protocol, habitat management and restoration, population viability, and accurate measures of population recruitment (Hamerstrom and Hamerstrom 1957, Pusateri 1990, Keir 1999, Walk 2004).

In USFS Region 2, the Land and Resource Management Plan for the Nebraska National Forest (applicable to the Samuel R. McKelvie and Fort Pierre National Grasslands) has guidelines for management of greater prairie-chicken habitat (Cables 2001). Specific recommendations include:

- ❖ Prohibit construction within 0.4 km of leks.
- ❖ Prohibit disturbance (construction, gravel mining, drilling of water wells, training of hunting dogs) within 1.6 km of leks between 1 March and 15 June.
- ❖ Manage viewing activities on leks to reduce disturbance.
- ❖ Design and implement livestock grazing strategies that provide quality nesting and

brooding habitat on at least 30% of the area within 1.6 km of leks.

- ❖ Do not plant trees in prairie-chicken habitat (not including native shrubs).

Larger, more contiguous tracts of greater prairie-chicken habitat have been maintained in Region 2 than in eastern parts of the greater prairie-chicken range as climate, topography, and soil conditions are more favorable for livestock production than cultivation. In South Dakota, Rice and Carter (1982) examined the effects of different stocking rates and grazing management systems on the habitat used for nesting and brood rearing. Height and density of ungrazed forage was influenced by both the grazing system and stocking rate. When range sites were combined, the amount of ungrazed forage was significantly greater in rest-rotation than deferred-rotation systems. They determined that the amount of ungrazed forage was related to AUM usage. However, despite having the lowest acres per AUM, the rest-rotation grazing system still had greater amounts of ungrazed forage than the deferred-rotation system. Comparisons among the different grazing systems found that the nest-brood use averaged 10.1 nests-broods per 1000 acres in the winter pastures (900 lbs. ungrazed forage per acre), and 9.3 nests-broods per 1000 acres in rest-rotation ungrazed allotments (950 lbs. ungrazed forage per acre). The fewest nests-broods were found in deferred rotation systems, 0.8 nests-broods per 1000 acres (450 lbs. ungrazed forage per acre).

During the 1960s, numbers of greater prairie-chickens on the Shesenne National Grassland were extremely low (total of three to nine males per year), and the entire area was grazed season long (Kobriger et al. 1988). The population did not show an increase until rotational grazing practices and prescribed burns were started on some of the allotments in the late 1960s and early 1970s. Numbers of greater prairie-chickens increased when allotments were changed from season-long grazing to deferred and rotational systems (1968 to 1978). Throughout most of this time, prescribed burns were also used to control woody vegetation. Peak number of displaying males reached 420 during 1980, but the population began to fluctuate erratically following several changes in the grazing practices, reduction in prescribed burning, and implementation of a short-duration rotational system (Kobriger et al. 1988). Peak numbers on the Valentine National Wildlife Refuge in Nebraska occurred when the number of AUMs was reduced from more than 50,000 to less than 10,000 (Svedarsky and Van Amburg 1996).

Although grazing systems can influence populations of greater prairie-chickens, they are of limited value if the stocking rates are too high (Svedarsky and Van Amburg 1996); heavy stocking rates reduce the ecological condition of the rangeland (Holechek et al. 1999) and result in reduced landscape heterogeneity (Fuhlendorf and Engle 2001). Holechek et al. (1999) reviewed 25 rangeland grazing studies and determined that reducing the stocking rate from heavy to moderate resulted in increased grazing capacity of the rangeland. Additionally, during drought years rangeland managed with light to moderate grazing had greater average forage production (lbs. per acre) than areas heavily grazed.

In recent years, considerable quantities of cropland in Region 2 have been enrolled in federal programs such as the CRP and the Environmental Quality Incentives Program (EQIP; Wildlife Habitat Management Institute 1999, Riley 2004). The lack of suitable grasslands is a primary reason why implementation of the CRP is believed to have had a positive effect on greater prairie-chicken range in many parts of Region 2. The conversion of some grain fields to grasslands may increase the quantity and quality of available nesting and roosting habitat (Fredrickson et al. 1999, Giesen and Schroeder 1999, Vodehnal 1999). These increases have been particularly significant in areas where native, warm-season grasses have been planted (Svedarsky et al. 2000). The restoration of prairie habitats with these incentives represents a broad-scale change in land use, and has the potential to dramatically improve habitat and landscape conditions for greater prairie-chickens. In some areas, however, such as the Flint Hills of Kansas, conversion of many of the grain fields to grasslands has potentially reduced the availability of grain (Rodgers et al. 2000). As well, the shift from primarily sorghum to soybean production in the Flint Hills may have adversely affected the quality of winter habitat in this area (Rodgers et al. 2000).

In Region 2, conditions of excessive winter snow cover may limit food availability for greater prairie-chickens, and it is during these times when access to grain fields may be important (Svedarsky et al. 2000). For instance, greater prairie-chickens in Yuma County, Colorado typically began feeding in corn fields after the first substantial snow fall and if the snow melted, birds were observed less frequently in the corn fields. Once snow cover was permanent, greater prairie-chickens used the corn fields regularly and could be captured by baiting walk-in traps with ears of dried corn (Schroeder and Braun 1992a), similar to findings from Wisconsin (Hamerstrom and Hamerstrom 1973). Greater prairie-

chickens also use grain fields during spring. Incubating females have been observed foraging in corn fields, but it is not clear if they are feeding exclusively on grain or other foods (e.g., new vegetative growth, insects) available at these sites (Schroeder and Braun 1992a).

Prescribed burning to control woody vegetation and/or rejuvenate herbaceous cover can positively affect greater prairie-chicken habitat, especially in the eastern part of the range (Grange 1948, McKee et al. 1998, Svedarsky et al. 2000). Greater prairie-chicken range in Minnesota occurs in the transition zone of the continental forest-prairie habitat where grasslands are a sub-climax plant community and prescribed burning is a necessary management tool for maintaining grassland areas (Svedarsky et al. 1999). Most of greater prairie-chicken range in Region 2 is situated in the Great Plains-Dry Steppe and Great Plains Steppe zones, which are grassland habitats with primarily shortgrass and tallgrass species. Eastern Nebraska and Kansas lie in the Prairie Parkland zone where the vegetation is classed as forest-steppe; prairie grasslands in these areas are believed to have been historically maintained by frequent fires.

If the minimum number of males needed in a population is assumed to be 250 and the density estimates of 0.3 to 2.5 males per km² are representative, then the area needed to support a viable population of greater prairie-chickens ranges from 100 to 833 km². Hamerstrom et al. (1957:18) recommended management for greater prairie-chickens on “nothing less than half a township [about 50 km²], except as a last resort, and more if hunting is anticipated.” Although, the 50 km² estimate is less than the 100 km² figure given above, Hamerstrom et al. (1957) recognized the importance of integrating both public and private ownerships and multiple land uses in a large area where density of greater prairie-chickens would not be expected to be uniform across the landscape. They believed a “scatter-pattern” of necessary cover would “produce more greater prairie-chickens” than a solid, but smaller, block of habitat (Hamerstrom et al. 1957:62). They provided an assessment of numerous management options in central Wisconsin including the recommended structuring of landscapes, guidelines for acquiring and managing habitats including food plots, and suggestions for monitoring and harvesting populations. A recent evaluation of the greater prairie-chicken populations in central Wisconsin (Anderson and Toepfer 1999) has indicated that the earlier proposals were in many ways successful. However, although the central Wisconsin populations have persisted, recent genetic studies indicate that they show

signs of genetic isolation (Johnson et al. 2003, 2004). This indicates that the scatter-patterning approach, by itself, is not adequate to assure persistence of viable greater prairie-chicken populations (Applegate et al. 2004). The most stable portion of the primary management area (Buena Vista Marsh) was about four times as large as the minimum recommended area (total of about 200 km²). In contrast, the population in Leola Marsh (about 50 km²) appeared to show long-term declines (Anderson and Toepfer 1999). Because it could be argued that a 50 km² area is insufficient to support a viable population of greater prairie-chickens, recommendations of management areas of 6 to 16 km² (Toepfer et al. 1990, Westemeier and Gough 1999) appear to be unrealistic without intensive intervention, such as population augmentations.

Although these estimates of necessary management areas (100 to 833 km²) may appear large and impractical, the vast majority of evidence across the range of the greater prairie-chicken shows that small and isolated populations inevitably decline toward extinction. The Attwater's prairie-chicken can be used to illustrate this trend (Silvy et al. 1999). In 1980, at least seven populations were found on a total of 1,204 km², the vast majority of which was not managed for prairie-chickens. The largest population contained 726 males on about 495 km². By 1998, only six males were observed on 32 km². All but two of the populations were extinct, with the largest consisting of about 18 males (Silvy et al. 1999). The recovery plan for the Attwater's prairie-chicken (U.S. Fish and Wildlife Service 1993) recommended acquisitions, easements, and management actions on larger areas than were ultimately involved, illustrating the importance of large management areas.

These estimates of the size of management areas assume that the habitat is suitable and meets the needs of greater prairie-chickens. Considerations of landscape heterogeneity, such as the spatial and temporal distribution of nesting, roosting, and brooding habitats may increase the area requirements (Westemeier and Gough 1999). In Region 2, areas that could potentially support greater prairie-chickens do not because of land use practices that eliminate or reduce nest, brood, roost, and escape cover (Fredrickson et al. 1999, Vodehnal 1999). Capacity of rangeland to support greater prairie-chickens is significantly influenced by some grazing practices and annual burning (Rice and Carter 1982, Kobriger et al. 1988, Applegate and Horak 1999). Additionally, traditional range management practices may decrease rangeland heterogeneity by encouraging plant species that are most productive and

palatable for livestock (Fuhlendorf and Engle 2001). Differences among nest, brood, roost, and lek habitats suggest that heterogeneity of the rangeland may be an important factor in determining the capacity of an area to support greater prairie-chickens. Areas with some type of disturbance may be important for lek sites and brood areas; however, areas of undisturbed cover are important for nesting and roosting.

Populations of greater prairie-chickens outside the core areas in Region 2 are believed to be relatively small and localized (Westemeier and Gough 1999). Viability of these populations may be important in maintaining connectivity among the core areas in Region 2. Loss, fragmentation, and degradation of greater prairie-chicken habitat increase the probability of isolation of small populations and make them vulnerable to extinction. Small, isolated populations are susceptible to problems associated with loss of genetic diversity, such as decreased fitness, as has been shown for greater prairie-chickens in Illinois (Bouzat et al. 1997, Westemeier et al. 1998).

There have been many specific recommendations for the management of greater prairie-chicken populations and habitat. These include modification of specific grazing practices (Rice and Carter 1982, Manske et al. 1988, Westemeier and Gough 1999), removal of encroaching shrubs and trees (McKee et al. 1998, Svedarsky et al. 2000), provision of food plots (Hamerstrom et al. 1957), retention of residual vegetation near leks (Svedarsky et al. 2000), support of Conservation Reserve Program (Storch 2000), and reduction in density of ring-necked pheasants (Westemeier and Gough 1999, Svedarsky et al. 2000). Evaluation of these approaches has often shown that greater prairie-chicken responses were positive to the applied management. For example, alteration in the grazing system on the Shenyenne National Grassland (Kobriger et al. 1988) and reduction in the AUMs on the Valentine National Wildlife Refuge (Svedarsky and Van Amburg 1996) resulted in increases in bird numbers. In contrast, many of the other activities, such as reduction in shrub/tree densities and protection of residual cover, have been difficult to evaluate because the expected effects were small, cumulative, and anecdotal.

Declines in populations and genetic heterogeneity have been used to justify efforts to augment and/or re-establish populations. The greater prairie-chicken recovery plan for Colorado (Pusateri 1990) and the U.S. Fish and Wildlife Service (1993) recovery plan for the Attwater's prairie-chicken both recommend translocations as an integral component of recovery

efforts. The Attwater's prairie-chicken plan also recommends rearing captive birds as an additional technique. Although captive-rearing has not yet been shown to be successful (Silvy et al. 1999), translocations of wild birds have been successful in many areas (Toepfer et al. 1990, Hoffman et al. 1992, Westemeier et al. 1998, Moe 1999). In some cases, the translocations of greater prairie-chickens helped to re-establish populations in formerly occupied range (northeastern Colorado and south-central Iowa). In other situations, they have added genetic heterogeneity to populations that were too small and isolated to be viable over the long-term (Illinois). Translocations have also been incorporated into a conservation genetics management plan for greater prairie-chickens in Wisconsin (Bouzat et al. 2005).

Inventory and monitoring

Population monitoring: Surveys to locate greater prairie-chickens are conducted during the early spring when males are congregated on lek sites. Survey protocol generally follows the methodology outlined by Hamerstrom and Hamerstrom (1973), but various state agencies have modified this protocol to accommodate funding and personnel available to complete the surveys. Survey efforts generally last a month and overlap the peak in female lek attendance (often early to mid-April; Applegate and Horak 1999, Vodehnal 1999). Surveys are conducted during the period when birds are most active, 45 minutes prior to sunrise and for 1 to 2 hours after sunrise (Hamerstrom and Hamerstrom 1973). Calm, clear mornings are best, as the booming sound produced by males can be audible for approximately 3 km (Hamerstrom and Hamerstrom 1973). On survey routes, an observer determines the presence of active lek site by listening at 1.6 km intervals along a predetermined survey route (16 to 32 km long) and recording all audible leks within a 1.6 km radius of the stop (Applegate and Horak 1999, Fredrickson et al. 1999, Vodehnal 1999). Leaks detected along the survey route and leks known to be active in previous years are then visited on one or two occasions, and the number of birds present is recorded (Applegate and Horak 1999, Vodehnal 1999). Other surveys usually consist of a complete survey of all the leks in a given area, and counts of the birds present on those leks (Hamerstrom and Hamerstrom 1973, Christisen 1985, Schroeder and Braun 1992b). In addition to annual survey routes, Breeding Bird Survey (BBS) data and Audubon Christmas Bird Counts (CBC) provide additional information regarding the regional distribution of greater prairie-chickens. However, BBS routes are not uniformly distributed throughout Region 2, and CBC

counts are typically centered near developed areas (e.g., towns, cities) and are conducted during December when birds may be more difficult to detect.

Surveys conducted by state agencies often use roads as transect routes. However, roadways are not randomly distributed throughout potential greater prairie-chicken habitat, possibly leading to biases in interpretation of data collected (Applegate 2000). Additionally, leks may be missed or under-represented on survey routes. For example, permanent leks may be easier to detect than temporary leks (Schroeder and Braun 1992b), and detection of leks may be more difficult in fragmented habitats. Differences in observer effort (time spent conducting surveys) and timing of lek surveys (fewer leks are detected later in the morning display period) may also affect survey route information and be a problem in some areas (Applegate 2000). In general, information gathered from various sources is used to evaluate and determine distributional changes for prairie grouse. These sources include historical records, published literature, agency survey data, hunter returns, miscellaneous observations, and presence of available and suitable habitat (Schroeder et al. 2004).

The work of Hamerstrom and Hamerstrom (1973) in Wisconsin summarizes the findings of the first long-term study of a marked population of greater prairie-chickens. The Hamerstoms were assisted by more than 5,000 volunteers (almost 7,000 person-mornings) who helped them to intensively monitor the activity of birds at all lek sites on the study area. Efforts were so consistent and concentrated that individual greater prairie-chickens could sometimes be identified from unique plumage coloration patterns (Hamerstrom and Hamerstrom 1973). Intensive monitoring of populations comparable to what the Hamerstoms accomplished is neither logistically nor financially feasible for a region-wide assessment of greater prairie-chicken population abundance. Instead, state wildlife agencies in Region 2 have tended to conduct lek survey routes through occupied greater prairie-chicken range to determine an index of population abundance. In many states, these surveys have been run for several decades, and the densities of leks and the attendance of males at leks have been used as indices of population change (Hamerstrom and Hamerstrom 1973, Horak 1985, Kobriger et al. 1988). Cannon and Knopf (1981) suggested that lek density, instead of the number of males on leks, could be used to derive a lek index that reflected population changes and recommended that surveys encompass areas of at least 2100 to 4200 ha (for example, see Schroeder et al. 1992). However, typical lek surveys use roads as transect routes and monitor

the leks on the route, not all the leks in a defined area as suggested by Cannon and Knopf (1981, however see Anderson and Toepfer 1999). As well, though the transect route may be randomly selected, roads are not randomly distributed through greater prairie-chicken habitat. Roads may also create edge habitats that influence greater prairie-chicken behavior (Applegate 2000). Leks surveys assume that all leks on a survey route are equally detectable, but detection of permanent leks may differ from temporary leks and lek sites may shift among years and consequently not be detected on the transect (Schroeder and Braun 1992b). Various other factors such as weather (Hamerstrom and Hamerstrom 1973), timing (date and time of day) (Robel 1967, Schroeder and Braun 1992b), predators (Berger et al. 1963, Hamerstrom et al. 1965), and observer bias (Applegate 2000) may also influence detection of leks. Local changes in lek densities and male lek attendance are also assumed to represent changes at a broader scale, which may not be valid. For instance, fluctuations in lek visitation are more likely to be caused by local rather than regional changes in the pattern of male lek attendance (Schroeder and Braun 1992b). Additionally, accuracy of male lek attendance data is influenced by numerous factors, such as method used to determine the count (flushing vs. observation), lek stability, timing (date and time), and number of surveys conducted (Schroeder and Braun 1992b, Applegate 2000). Furthermore, estimates of lek density and male attendance are rarely determined with a corresponding estimate of precision (Schroeder and Braun 1992b).

Despite the potential problems with lek surveys, they appear to offer the best opportunity to monitor populations over the long-term (Schroeder and Braun 1992b). Connelly et al. (2004) showed that data collected with counts of greater sage-grouse leks were defensible in evaluating long-term trends. It also is likely that monitoring sage-grouse leks is more problematic than monitoring greater prairie-chicken leks due to the higher variability and lower male visitation rates of sage-grouse (Jenni and Hartzler 1978, Emmons and Braun 1984, Schroeder and Braun 1992b, Walsh et al. 2004). Even so, it is important to recognize the limits of lek survey data as a method of monitoring greater prairie-chicken populations. Lek survey data can be used to determine the presence or absence of greater prairie-chickens in potential habitat and to provide indices of population change (Applegate 2000). Whether these indices represent local or broad scale changes depends on the sampling design, i.e. stratification of the survey routes, number of transects, and/or areas surveyed. For instance, lek surveys in Nebraska are currently conducted only in the Sandhills,

and the relationship between trends observed there and populations in other parts of the state are unclear. Additionally, simply multiplying number of birds per area by the area of total occupation does not account for the effect of habitat fragmentation (Walsh 1995).

Habitat monitoring: Important aspects of habitat monitoring are the measurements used and their scale and timing. Johnson (1980) described habitat selection as a hierarchical process and used different levels of selection to illustrate this process. First-order selection represents the geographic range; second-order selection represents the home range; third-order selection represents the use of the different habitat components in the home range; fourth-order selection represents the use of specific resources in these habitats. These orders range from macro-scale to micro-scale components of habitat selection, and examination of both scales is important for understanding animal-habitat relationships (Litvaitis et al. 1994).

At the broadest scale, habitat data can be collected by maps, aerial photographs, and satellite imagery (Litvaitis et al. 1994, Samson et al. 2004). This scale of resolution provides general information regarding the distribution of the major habitat types occupied or potentially occupied by greater prairie-chickens. Satellite imagery can refine this picture further by discerning the degree of fragmentation within the general range. As well, satellite imagery can indicate changes in habitat type over time, for example conversion of native grassland habitat to agriculture or conversion of cropland to CRP. However, in some cases confusion may occur among land-cover classes with similar spectral characteristics (Washington Department of Fish and Wildlife 2000). General habitat surveys also tend to report areas by vegetation type rather than by condition, even though the condition of occupied and potential habitat plays a major role in the distribution and abundance of greater prairie-chickens.

The next level of resolution is to examine greater prairie-chicken habitat at a local scale, where birds occur (**Figure 20**). At the local scale factors such as habitat patch size and configuration in the landscape, vegetation type and succession, cover density and height, and juxtaposition of habitats are important variables to monitor. Within greater prairie-chicken homes ranges, practices such as grazing, farming, mowing, burning, and spraying all influence the availability of resources and how birds use habitat. To monitor the effects of habitat at the local scale, sampling could be done through stratified sampling of areas of low, medium, and high greater prairie-chicken densities. These areas



Figure 20. Site-specific habitat assessment often requires an examination of shrub, grass, and forb cover.

and the habitats they encompass would be monitored simultaneously to evaluate population responses to various habitat variables.

Numerous techniques have been employed to address specific features of greater prairie-chicken habitat, such as species composition and cover and height of grasses, shrubs, forbs, and residual vegetation. These techniques include, but are not limited to, line intercept (Canfield 1941), point intercept (Evans and Love 1957), Daubenmire plot (Daubenmire 1959), point intercept frame (Floyd and Anderson 1982), and ocular estimate (Daubenmire 1968). Although there has not been a clear effort to standardize sampling techniques across the range (see Connelly et al. 2003 for greater sage-grouse example), the height-density-index (VOR, a horizontal 'visual obstruction reading' measured in decimeters; Robel et al. 1970a, Benkobi et al. 2000) perhaps comes the closest. Benkobi et al. 2000 found a strong relationship between the visual obstruction of standing vegetation and the weight of dried/clipped vegetation in the sandy lowland range sites of the Nebraska Sandhills. They suggested that the visual obstruction technique is an economical way to monitor large areas of grassland for average standing crop.

Information Needs

Greater prairie-chickens have been studied for many decades. However, various aspects of their biology and ecology, at broad and local scales, need further understanding. Greater prairie-chicken populations in Region 2 have been monitored for many years, providing general information regarding the historical and current distributions of populations. However, in some areas, there is little monitoring of localized populations. Assessment of areas that connect the core populations in South Dakota, Colorado, Nebraska, and Kansas are important for evaluating the long-term persistence of greater prairie-chickens in Region 2.

An accurate range-wide assessment of the distribution and abundance of greater prairie-chickens and their habitats is critical for the implementation and evaluation of management or conservation plans. In particular, specific information on population size and connectivity is needed. This is important since populations may cross political boundaries and require cooperative management efforts among numerous agencies. Lek survey data are used as indices of population change thus the development and implementation of a standardized, statistically

valid technique is needed to monitor population densities of greater prairie-chickens (Schroeder and Braun 1992b). Accurate estimates of greater prairie-chicken populations are needed to evaluate and monitor management strategies at both the broad and local scales in Region 2. Accurate information regarding sex ratios, male and female lek attendance, and lek stability is needed. Even more importantly, this necessitates the establishment of a relationship between survey results and actual long-term trends (Connelly et al. 2004, Walsh et al. 2004).

The metapopulation dynamics of greater prairie-chicken populations need to be examined. This will require an improved understanding of the relationship between behavior (e.g., dispersal, migration, home range), seasonal habitat selection, and characteristics of the habitat (e.g., quality, quantity, configuration). In addition, the genetic ramifications of population isolation need to be quantified.

At both the broad and local scale the relationship between greater prairie-chickens and habitat needs further understanding. Considerations of habitat quantity, quality, configuration, fragmentation, seasonal habitat needs, and limiting factors are all important. Habitat fragmentation is increasingly common within the range of greater prairie-chickens, and accurate information is needed regarding aspects of habitat use (patterns of movement, patch size) and nest-brood success in fragmented landscapes. The nest-brood period can be a demographic “bottle-neck” for greater prairie-chickens, so it is important to understand how habitat can mitigate mortality factors during this period. Buffer areas are often designated around active lek sites.

For example in some areas development is prohibited within 400 m of a lek site (Cables 2001), however this distance only considers direct disturbance to birds on or near the lek, not to the surrounding nesting and brood rearing habitat.

In recent years considerable cropland acreage in Region 2 has been enrolled in the CRP and replanted to grasslands. The CRP enrollments represent broad scale changes in land use, and it is important to understand how greater prairie-chicken populations have responded to these changes and the relative importance of different CRP lands (quality and quantity).

Grazing of rangeland can significantly impact greater prairie-chicken populations. Grazing practices that are economically feasible for livestock producers and beneficial for greater prairie-chickens need to be determined. It is important that this research first focus on livestock management practices in the vast areas that need restoration for greater prairie-chickens rather than testing grazing practices in areas that currently support greater prairie-chickens.

Prairie systems have been largely converted for the production of row crops across the Great Plains, and the few remaining patches of prairie have been subdivided with fences into grazing allotments. Samson et al. (2004:11) suggested that “fences are the problem in, not the solution to, conservation of historically grazed ecosystems.” In any case, research on the restoration of prairie ecosystems is desperately needed, not only for the greater prairie-chicken, but for the many other species of wildlife that depend on grasslands for their survival (Rich et al. 2004, Samson et al. 2004).

DEFINITIONS

The terms “use,” “selection,” and “preference” generally are used when examining the relationship between a species and its habitat. “Use” indicates an association with a resource; “selection” implies actively choosing a particular resource from an available range of options (Johnson 1980, Litvaitis et al. 1994). Habitat selection occurs at a broad range of scales; macro-scale characteristics include biogeographic and home range, and micro-scale characteristics include specific features at use sites such as stem density, canopy cover height, and percent bare ground (Johnson 1980, Litvaitis et al. 1994). “Preference” for a particular resource is determined independent of its availability and usually is evaluated by experimental manipulation, such as with habitat exclosures (Litvaitis et al. 1994).

REFERENCES

- Addison, E.M. and R.C. Anderson. 1969. *Oxyspirura* n. sp. (Nematoda: Thelaziidae) from Tetraonidae in North America. *The Canadian Journal of Zoology* 47:1223-1227.
- Aldous, S.E. 1943. Sharp-tailed grouse in the sand dune country of north-central North Dakota. *Journal of Wildlife Management* 7:23-31.
- Aldrich, J.W. 1963. Geographic orientation of American Tetraonidae. *Journal of Wildlife Management* 27:529-545.
- Aldrich, J.W. and A.J. Duvall. 1955. Distribution of American gallinaceous game birds. United States Department of the Interior, Fish and Wildlife Service, Circular 34.
- American Ornithologists' Union. 1957. Check-list of North American birds. 5th edition. American Ornithologist's Union, Washington, D.C.
- American Ornithologists' Union. 1983. Check-list of North American birds. 6th edition. American Ornithologist's Union, Washington, D.C.
- Ammann, G.A. 1957. The prairie grouse of Michigan. Michigan Department of Conservation, P-R Report, Projects W-5-R, W-37-R, and W-70-R.
- Anderson, R.K. 1969. Greater prairie-chicken responses to changing booming-ground cover type and height. *Journal of Wildlife Management* 33:636-643.
- Anderson, R.K. and J.E. Toepfer. 1999. History, status, and management of the greater prairie-chicken in Wisconsin. Pages 39-58 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. *The greater prairie-chicken a national look*. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Andrewartha, H.G. and L.C. Birch. 1984. *The ecological web: more on the distribution and abundance of animals*. University of Chicago Press, Chicago, IL.
- Angelstam, P. 1983. Population dynamics of tetraonids, especially the black grouse *Tetrao tetrix* L., in boreal forests. Ph.D. Thesis, Uppsala University, Uppsala, Sweden.
- Angelstam, P.K. 1988. Population dynamics in tetraonids: the role of extrinsic factors. Pages 2458-2477 in H. Ouellet, editor. *Acta XIX Congressus Internationalis Ornithologici*. University of Ottawa Press, Canada.
- Applegate, R.D. 2000. Use and misuse of prairie chicken lek surveys. *Wildlife Society Bulletin* 28:457-459.
- Applegate, R.D. and G.J. Horak. 1999. Status and management of the greater prairie-chicken in Kansas. Pages 113-122 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. *The greater prairie-chicken a national look*. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Applegate, R.D., C.K. Williams, and R.R. Manes. 2004. Assuring the future of prairie grouse: dogmas, demagogues, and getting outside the box. *Wildlife Society Bulletin* 32:104-111.
- Arthaud, F.L. 1970. Land use and greater prairie-chicken populations in southwestern Missouri. *Transactions of the Kansas Academy of Science* 73:267-276.
- Atyeo, W.T. and J. Gaud. 1992. The identity of *Pterolichus obtusus* Robin, 1877 with descriptions of new genera and species of feather mites (Acarina, Pterolichidae) from the Galliformes (Aves). *Acarologia* 33:193-206.
- Baker, M.F. 1953. Greater prairie-chickens of Kansas. University of Kansas Museum of Natural History and State Biological Survey, Miscellaneous Publications Number 5.
- Beidleman, C.A. 2000. Partners in Flight land bird conservation plan Colorado. Version 1.0. Partners in Flight.
- Bellinger, M.R., J.A. Johnson, J. Toepfer, and P. Dunn. 2003. Loss of genetic variation in greater prairie chickens following a population bottleneck in Wisconsin, U.S.A. *Conservation Biology* 17:717-724.

- Benkobi, L., D. W. Uresk, G. Schenbeck, and R. M. King. 2000. Protocol for monitoring standing crop in grasslands using visual obstruction. *J. Range Management* 53:627-633.
- Berger, D.D., F. Hamerstrom, and F.N. Hamerstrom, Jr. 1963. The effect of raptors on prairie chickens on booming grounds. *Journal of Wildlife Management* 27:778-791.
- Bergerud, A.T. 1988a. Increasing the numbers of grouse. Pages 686-731 in A.T. Bergerud and M.W. Gratson, editors. *Adaptive strategies and population ecology of northern grouse*. The Wildlife Management Institute. University of Minnesota Press, Minneapolis, MN.
- Bergerud, A.T. 1988b. Population ecology of North American grouse. Pages 578-685 in A.T. Bergerud and M.W. Gratson, editors. *Adaptive strategies and population ecology of northern grouse*. The Wildlife Management Institute. University of Minnesota Press, Minneapolis, MN.
- Blus, L.J. and J.W. Walker. 1966. Progress report on the prairie grouse nesting study in the Nebraska sandhills. *Nebraska Bird Review* 36:23-30.
- Blus, L.J., C.S. Staley, C.J. Henny, G.W. Pendleton, T.H. Craug, E.H. Craig, and D.K. Halford. 1989. Effects of organophosphorus insecticides on sage grouse in southwestern Idaho. *Journal of Wildlife Management* 53: 1139-1146.
- Boag, D.A., and M.A. Schroeder. 1992. Spruce grouse *Dendragapus canadensis*. In: A. Poole, P. Stettenheim, and F. Gill, editors. *The Birds of North America*, Number 5. Philadelphia: The Academy of Natural Sciences, Washington, D.C.: The American Ornithologists' Union.
- Bouzat, J.L., H.H. Cheng, H.A. Lewin, R.L. Westemeier, J.D. Brawn, and K.N. Paige. 1997. Genetic evaluation of a demographic bottleneck in the greater prairie-chicken. *Conservation Biology* 12:836-843.
- Bouzat, J.L., P. Dunn, S. Haig, J.A. Johnson, S. Oyler-McCance, B.L. Sloss, and B.J. Swanson. 2005. Conservation genetics plan for the management and recovery of greater prairie-chickens in Wisconsin. Wisconsin Department of Natural Resources, Madison, WI.
- Bowman, T.J. and R.J. Robel. 1977. Brood break-up, dispersal, mobility, and mortality of juvenile greater prairie-chickens. *Journal of Wildlife Management* 41:27-34.
- Bradbury, J.W. 1981. The evolution of leks. Pages 138-169 in R.D. Alexander and D.W. Tinkle, editors. *Natural Selection and social behavior: recent research and new theory*. Chiron Press, New York, NY.
- Braun, C.E., K. Martin, and L.A. Robb. 1993. White-tailed ptarmigan (*Lagopus leucurus*). In: A. Poole and F. Gill, editors. *The Birds of North America*, Number 68. Philadelphia: The Academy of Natural Sciences, Washington, D.C.: The American Ornithologists' Union.
- Buhnerkempe, J.E., W.R. Edwards, D.R. Vance, and R.L. Westemeier. 1984. Effects of residual vegetation on greater prairie-chicken nest placement and success. *Wildlife Society Bulletin* 12:382-386.
- Burger, L.W., M. Ryan, and D.P. Jones. 1989. Prairie-chicken ecology in relation to landscape patterns. *Missouri Prairie Journal* 11:13-15.
- Cables, R.D. 2001. Land and resource management plan for the Nebraska National Forest and associated units. USDA Forest Service, Rocky Mountain Region. Lakewood, CO.
- Cables, R.D. 2002. Final environmental impact statement and land and resource management plan. Record of decision. Nebraska and Samuel R. McKelvie National Forests, Oglala, Buffalo Gap, and Fort Pierre National Grasslands. USDA Forest Service, Rocky Mountain Region. Chadron, NE.
- Canfield, R.H. 1941. Application of the line interception method in sampling range vegetation. *Journal of Forestry* 39: 388-394.
- Cannon, R.W. and F.L. Knopf. 1981. Lek numbers as a trend index to prairie grouse populations. *Journal of Wildlife Management* 45:776-778.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. Second Edition. Sinauer Associates, Inc., Sunderland, MA.

- Christisen, D.M. 1969. National status and management of the greater prairie-chicken. Transactions of the 34th North American Wildlife and Natural Resources Conference 34:207-217.
- Christisen, D.M. 1985. The greater prairie-chicken and Missouri's land use patterns. Missouri Department of Conservation, Terrestrial Series Number 15.
- Connelly, J.W., A.D. Apa, R. B. Smith, and K.P. Reese. 2000. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. Wildlife Biology 6:227-232.
- Connelly, J.W., M.W. Gratson, and K.P. Reese. 1998. Sharp-tailed grouse (*Tympanuchus phasianellus*). In: A. Poole and F. Gill, editors. The Birds of North America, Number 354. The Birds of North America, Inc., Philadelphia, PA.
- Connelly, J.W., S.T. Knick, M.A. Schroeder, and S.J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Cheyenne, WY.
- Connelly, J.W., K.P. Reese, and M.A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. University of Idaho, College of Natural Resources Experiment Station Bulletin 80. Moscow, ID.
- Cram, E.B. 1937. A review of the genus *Oxyspirura* with a morphological study of *O. petrowi* Skrjabin, 1929, recently discovered in galliform birds on the northern United States. Pages 89-98 in Papers on helminthology published in commemoration of the 30 Year Jubileum of the scientific, educational, and social activities of the honored worker of science K. I. Skrjabin and of the fifteenth anniversary of the All-Union Institute of Helminthology, Moscow, USSR.
- Daubenmire, R.F. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33:43-64.
- Daubenmire R.F. 1968. Plant communities: a textbook of plant synecology. Harper and Rowe, Publishers, New York, NY.
- Dobson, A.P., E.R. Carper, and P.J. Hudson. 1988. Population biology and life-history variation of gamebirds. Pages 48-71 in P.J. Hudson and M.R.W. Rands, editors. Ecology and management of gamebirds. Blackwell Scientific Publications Professional Books, Oxford, UK.
- Drew, M.L., W.L. Wigle, D.L. Graham, C.P. Griffin, N.J. Silvy, A.M. Fadly, and R.L. Witter. 1998. Reticuloendotheliosis in captive greater and Attwater's prairie chickens. Journal of Wildlife Diseases 34:783-791.
- Drobney, R.D. and R.D. Sparrowe. 1977. Land use relationships and movements of greater prairie-chickens in Missouri. Transactions, Missouri Academy of Science 10-11:146-160.
- Drovetski, S.V. 2002. Molecular phylogeny of grouse: individual and combined performance of W-linked, autosomal, and mitochondrial loci. Systematics Biology 51:930-945.
- Drovetski, S.V. 2003. Plio-Pleistocene climatic oscillations, Holarctic biogeography and speciation in an avian subfamily. Journal of Biogeography 30:1173-1181.
- Elliott, D.L., C.G. Holladay, W.R. Barchet, H.P. Foote, and W.F. Sandusky. 1987. Wind energy resource atlas of the United States. DOE/CH 10093-4, Solar Energy Research Institute, Golden, CO.
- Ellsworth, D.L., R.L. Honeycutt, and N.J. Silvy. 1995. Phylogenetic relationships among North American grouse inferred from restriction endonuclease analysis of mitochondrial DNA. The Condor 97:492-502.
- Ellsworth, D.L., R.L. Honeycutt, N.J. Silvy, K.D. Rittenhouse, and M.H. Smith. 1994. Mitochondrial-DNA and nuclear-gene differentiation in North American prairie grouse (genus *Tympanuchus*). The Auk 111:661-671.
- Emerson, K.C. 1951. A list of Mallophaga from gallinaceous birds of North America. Journal of Wildlife Management 15:193-195.
- Emmons, S.R., and C.E. Braun. 1984. Lek attendance of male sage grouse. Journal of Wildlife Management 48:1023-1028.

- Eng, R.L., J.E. Toepfer, and J.A. Newell. 1988. Management of livestock to improve and maintain greater prairie-chicken habitat on the Sheyenne National Grasslands. Pages 55-72 in A.J. Bjugstad, technical coordinator. Greater prairie-chickens on the Sheyenne National Grasslands. United States Department of Agriculture Forest Service General Technical Report RM-159.
- Evans, K.E. 1966. Observations of a hybrid between the sharp-tailed grouse and the greater prairie-chicken. *The Auk* 83:128-129.
- Evans, K.E. 1968. Characteristics and habitat requirements of the greater prairie-chicken and sharp-tailed grouse - a review of the literature. United States Department of Agriculture Forest Service Conservation Report Number 12.
- Evans, K.E. and D.L. Gilbert. 1969. A method for evaluating greater prairie-chicken habitat in Colorado. *Journal of Wildlife Management* 33:643-649.
- Evans, R.A. and R.M. Love. 1957. The step-point method of sampling - a practical tool in range research. *Journal of Range Management* 10:208-212.
- Ewens, W.J., P.J. Brockwell, J.M. Gani, and S.I. Resnick. 1987. Minimum viable population size in the presence of catastrophes. Pages 59-68 in M.E. Soulé, editor. *Viable population for conservation*. Cambridge University Press, UK.
- Faanes, C.A. 1987. Bird behavior and mortality in relation to power lines in prairie habitats. United States Fish and Wildlife Service. Fish and Wildlife Technology Report 7.
- Fitzgerald, J., B. Busby, M. Howery, R. Klataske, D. Reinking, and D. Pashley. 2000. Partners in Flight birds conservation plan for the Osage Plains (physiographic area 33). Version 1.0. Partners in Flight.
- Fitzgerald, J.A. and D.N. Pashley. 2000. Partners in Flight bird conservation plan for the Dissected Till Plains (physiographic area 32). Version 1.0. Partners in Flight.
- Fitzgerald, J.A., D.N. Pashley, S.J. Lewis, and B. Pardo. 1998. Partners in Flight birds conservation plan for the Northern Tallgrass Prairie. Version 1.0. Partners in Flight.
- Fitzgerald, J.A., D.N. Pashley, and B. Pardo. 1999. Partners in Flight bird conservation plan for the Northern Mixed-grass Prairie (physiographic area 37). Version 1.0. Partners in Flight.
- Flanders-Wanner, B.L., G.C. White, and L.L. McDaniel. 2004. Weather and prairie grouse: dealing with effects beyond our control. *Wildlife Society Bulletin* 32:22-34.
- Floyd, D.A. and J.E. Anderson. 1982. A new point frame for estimating cover of vegetation. *Vegetation* 50:185-186.
- Fredrickson, L.F., B. Crouch, and G.L. Heismeyer. 1999. Status and management of greater prairie-chickens in South Dakota. Pages 75-80 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. *The greater prairie-chicken a national look*. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Fuhlendorf, S.D. and D.M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience* 51:625-632.
- Giesen, K.M. 1998. Lesser prairie-chicken (*Tympanuchus pallidicinctus*). In: A. Poole and F. Gill, editors. *The Birds of North America*, Number 364. The Birds of North America, Inc., Philadelphia, PA.
- Giesen, K.M. and M.A. Schroeder. 1999. Population status and distribution of greater prairie-chickens in Colorado. Pages 99-104 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. *The greater prairie-chicken a national look*. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Grange, W.B. 1948. Wisconsin grouse problems. Wisconsin Conservation Department, Madison, WI.
- Griffin, C.P., M.E. Morrow, and N.J. Silvy. 1997. Insects as a possible limiting factor for Attwater's prairie-chicken *Tympanuchus cupido attwateri*. (Abstract) *Wildlife Biology* 3:288.

- Gross, A.O. 1928. The heath hen. *Memoirs of the Boston Society of Natural History* 6:490-588.
- Gross, A.O. 1930. Progress report of the Wisconsin greater prairie-chicken investigation. Wisconsin Conservation Commission, Madison, WI.
- Gutiérrez, R.J., G.F. Barrowclough, and J.G. Groth. 2000. A classification of the grouse (Aves: Tetraoninae) based on mitochondrial DNA sequences. *Wildlife Biology* 6:205-211.
- Hagen, C.A., B.E. Jamison, K.M. Giesen, and T.Z. Riley. 2004. Guidelines for managing lesser prairie-chicken populations and their habitats. *Wildlife Society Bulletin* 32:69-82.
- Hamerstrom, F., D.D. Berger, and F.N. Hamerstrom, Jr. 1965. The effect of mammals on prairie chickens on booming grounds. *Journal of Wildlife Management* 29:536-542.
- Hamerstrom, F.N., Jr. 1939. A study of Wisconsin greater prairie-chicken and sharp-tailed grouse. *Wilson Bulletin* 51: 105-120.
- Hamerstrom, F.N., Jr. and F. Hamerstrom. 1949. Daily and seasonal movements of Wisconsin greater prairie-chickens. *The Auk* 66:313-337.
- Hamerstrom, F.N., Jr. and F. Hamerstrom. 1955. Population density and behavior in Wisconsin greater prairie-chickens (*Tympanuchus cupido pinnatus*). *Transactions of the International Ornithological Congress* 11:459-466.
- Hamerstrom, F.N., Jr. and F. Hamerstrom. 1960. Comparability of some social displays of grouse. *Transactions of the International Ornithological Congress* 12:274-293.
- Hamerstrom, F.N., Jr. and F. Hamerstrom. 1973. The greater prairie-chicken in Wisconsin - highlights of a 22 year study of counts, behavior, movements, turnover, and habitat. Wisconsin Department of Natural Resources. Technical Bulletin Number 64.
- Hamerstrom, F.N., Jr., F. Hopkins, and A.J. Rinzel. 1941. An experimental study of browse as a winter diet for greater prairie-chickens. *Wilson Bulletin* 53:185-195.
- Hamerstrom, F.N., Jr., O.E. Mattson, and F. Hamerstrom. 1957. A guide to greater prairie-chicken management. Wisconsin Conservation Department Technical Wildlife Bulletin Number 15. Madison, WI.
- Hannon, S.J. 1988. Intrinsic mechanisms and population regulation in grouse – a critique. Pages 2478-2489 in H. Ouellet, editor. *Acta XIX Congressus Internationalis Ornithologici*. University of Ottawa Press, Canada.
- Harper, G.R., R.D. Klataske, R.J. Robel, and M.F. Hansen. 1967. Helminths of greater prairie chickens in Kansas. *Journal of Wildlife Management* 31:265-269.
- Hier, R.H. 1999. History and hunting the greater prairie-chicken: a rich tradition. Pages 163-168 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. *The greater prairie-chicken a national look*. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Hjorth, I. 1970. Reproductive behavior in tetraonidae. *Viltrevy* 7:184-596.
- Hoffman, R.W., W.D. Snyder, G.C. Miller, and C.E. Braun. 1992. Reintroduction of greater prairie-chickens in northeastern Colorado. *Prairie Naturalist* 24:197-204.
- Höglund, J. and R.V. Alatalo. 1995. What are Lekks? Pages 3-22 in J.R. Krebs and T. Clutton-Brock, editors. *Leks*. Monographs in Behavior and Ecology. Princeton University Press, Princeton, NJ.
- Holechek, J.L., H. Gomez, F. Molinar, and D. Galt. 1999. Grazing studies: what we've learned. *Rangelands* 21(2): 12-16.
- Horak, G.J. 1985. Kansas greater prairie-chickens. Kansas Fish and Game Commission, Wildlife Bulletin Number 3.
- Horton, R.E. and D.H. Wolfe. 1999. Status and management of the greater prairie-chicken in Oklahoma. Pages 105-112 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. *The greater prairie-chicken a national look*. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.

- Hunt, J.L. 2004. Investigation into the decline of populations of the lesser prairie-chicken (*Tympanuchus pallidicinctus* Ridgway) in southeastern New Mexico. Ph.D. Dissertation, Auburn University, AL.
- Jenni, D.A. and J.E. Hartzler. 1978. Attendance at a sage grouse lek: implications for spring census. *Journal of Wildlife Management* 42:46-52.
- Johnsgard, P.A. 1983. *The grouse of the world*. University of Nebraska Press, Lincoln, NE.
- Johnsgard, P.A. and R.E. Wood. 1968. Distributional changes and interaction between greater prairie-chickens and sharp-tailed grouse in the Midwest. *Wilson Bulletin* 80:173-188.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Johnson, G.D. and M.S. Boyce. 1990. Feeding trials with insects in the diet of sage grouse chicks. *Journal of Wildlife Management* 54:89-91.
- Johnson, R.G. and S.T. Temple. 1990. Nest predation and brood parasitism of tallgrass prairie birds. *Journal of Wildlife Management* 54:106-111.
- Johnson, J.A., J.E. Toepfer, and P.O. Dunn. 2003. Contrasting patterns of mitochondrial and microsatellite population structure in fragmented populations of greater prairie-chickens. *Molecular Ecology* 12:3335-3347.
- Johnson, J.A., M.R. Bellinger, J.E. Toepfer, and P. Dunn. 2004. Temporal changes in allele frequencies and low effective population size in greater prairie-chickens. *Molecular Ecology* 13:In press.
- Jones, R.E. 1963. Identification and analysis of lesser and greater prairie-chicken habitat. *Journal of Wildlife Management* 27:757-778.
- Jones, R.E. 1964. The specific distinctness of the greater and lesser prairie chicken. *Auk* 81:65-73.
- Kay, C.E. 1998. Are ecosystems structured from the top-down or bottom-up? A new look at an old debate. *Wildlife Society Bulletin* 26:484-498.
- Keir, J.R. 1999. Wisconsin prairie chicken management: an agency perspective. Pages 59-62 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. *The greater prairie-chicken a national look*. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Kellogg, V.L. 1899. List of the biting lice (Mallophaga) taken from birds and mammals of North America. *Proceedings of the United States National Museum* 22(1183):39-100.
- Kirsch, L.M. 1974. Habitat management considerations for greater prairie-chickens. *Wildlife Society Bulletin* 2:124-129.
- Kirsch, L.M., A.T. Klett, and H.W. Miller. 1973. Land use and prairie grouse population relationships in North Dakota. *Journal of Wildlife Management* 37:449-453.
- Kobriger, G.D. 1965. Status, movements, habitats, and foods of prairie grouse on a sandhills refuge. *Journal of Wildlife Management* 29:788-800.
- Kobriger, J.D. 1999. Status and management of the greater prairie-chicken in North Dakota. Pages 63-74 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. *The greater prairie-chicken a national look*. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Kobriger, J.D., D.P. Vollink, M.E. McNeill, and K.F. Higgins. 1988. Greater prairie-chicken populations of the Sheyenne Delta in North Dakota, 1961-1987. Pages 1-7 in A.J. Bjugstad, technical coordinator. *Greater prairie-chickens on the Sheyenne National Grasslands*. United States Department of Agriculture Forest Service General Technical Report RM-159.
- Korschgen, L.J. 1962. Food habits of greater prairie-chickens in Missouri. *The American Midland Naturalist* 68:307-318.

- Lande, R.L. and G.F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pages 87-123 in M.E. Soulé, editor. Viable populations for conservation. Cambridge University Press.
- Lehmann, V.W. 1941. Attwater's prairie-chicken - its life history and management. United States Department of the Interior, Fish and Wildlife Service, North American Fauna 57.
- Leigh, W.H. 1940. Preliminary studies on parasites of upland game birds and fur-bearing mammals in Illinois. Illinois Natural History Survey Bulletin 21:185-194.
- Leigh, W.H. 1941. Variation in a new species of cestode, *Raillietina (Skrjabinia) variabila*, from the prairie-chicken in Illinois. Journal of Parasitology 27:97-106.
- Leopold, A. 1931. Report on a game survey of the North Central States. American Game Association, Madison, WI.
- Lincoln, F.C. 1950. A Ring-necked Pheasant x greater prairie-chicken hybrid. Wilson Bulletin 62:210-212.
- Litvaitis, J.A., K. Titus, and E.M. Anderson. 1994. Measuring vertebrate use of terrestrial habitats and foods. Pages 254-274 in T.A. Bookhout, editor. Research and management techniques for wildlife habitats. United States Fish and Wildlife Service, Ohio Cooperative Fish and Wildlife Research Unit. Ohio State University, Columbus, OH.
- Lutz, R.S., J.S. Lawrence, and N.J. Silvy. 1994. Nesting ecology of Attwater's prairie-chicken. Journal of Wildlife Management 58:230-233.
- Manske, L.L. and W.T. Barker. 1981. Greater prairie-chicken habitat use on the Sheyenne National Grasslands, North Dakota. Proceedings of the North Dakota Academy of Science 35:2.
- Manske, L.L. and W.T. Barker. 1988. Habitat usage by prairie grouse on the Sheyenne National Grasslands. Pages 8-20 in A.J. Bjugstad, editor, Prairie-chickens on the Sheyenne National Grasslands. U. S. Forest Service, General Technical Report, RM-159.
- McEwen, L.C., D.B. Knapp, and E.A. Hillard. 1969. Propagation of prairie grouse in captivity. Journal of Wildlife Management 33:276-283.
- McKee, G., M.R. Ryan, and L.M. Mechlin. 1998. Predicting greater prairie-chicken nest success from vegetation and landscape characteristics. Journal of Wildlife Management 62:314-321.
- Mechlin, L.M., R.W. Cannon, and D.M. Christisen. 1999. Status and management of greater prairie-chickens in Missouri. Pages 129-142 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. The greater prairie-chicken a national look. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Moe, M. 1999. Status and management of the greater prairie chicken in Iowa. Pages 123-127 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. The greater prairie-chicken a national look. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Mohler, L.L. 1952. Fall and winter habits of greater prairie-chickens in southwest Nebraska. Journal of Wildlife Management 16:9-23.
- Mohler, L.L. 1963. Winter surveys of Nebraska greater prairie-chickens and management implications. Journal of Wildlife Management 27:737-738.
- Morgan, B.B. and F.N. Hamerstrom, Jr. 1941. Notes on the endoparasites of Wisconsin pinnated and sharp-tailed grouse. Journal of Wildlife Management 5:194-198.
- Morrow, M.E., T.A. Rossignol, and N.J. Silvy. 2004. Federal listing of prairie grouse: lessons from the Attwater's prairie-chicken. Wildlife Society Bulletin 32:112-118.
- Naugle, D.E., C.L. Aldridge, B.L. Walker, T.E. Cornish, B.J. Moynahan, M.J. Holloran, K. Brown, G.D. Johnson, E.T. Schmidtman, R.T. Mayer, C.Y. Kato, M.R. Matchett, T.J. Christiansen, W.E. Cook, T. Creekmore, R.D. Falise, E.T. Rinkes, and M.S. Boyce. 2004. West Nile virus: pending crisis for greater sage grouse. Ecology Letters. In press.

- Newell, J.A., J.E. Toepfer, and M.A. Rumble. 1988. Summer brood-rearing ecology of the greater prairie-chicken on the Sheyenne National Grasslands. Pages 24-31 in A.J. Bjugstad, technical coordinator. Greater prairie-chickens on the Sheyenne National Grasslands. United States Department of Agriculture Forest Service General Technical Report RM-159.
- Osborn, H. 1896. Insects affecting domestic animals: an account of the species of importance in North America, with mention of related forms occurring on other animals. Bulletin of the United States Department of Agriculture, Division of Entomology, New Series Number 5.
- Paine, L., D.J. Undersander, D.W. Sample, G.A. Bartlett, and T.A. Schatteman. 1996. Cattle trampling of simulated ground nests in rotationally grazed pastures. *Journal of Range Management* 49:294-300.
- Peterson, M.J. 2004. Parasites and infectious diseases of prairie grouse: should managers be concerned? *Wildlife Society Bulletin* 32:35-55.
- Peterson, M.J. and N.J. Silvy. 1996. Reproductive stages limiting productivity of the endangered Attwater's prairie-chicken. *Conservation Biology* 10:1264-1276.
- Peterson, M.J., J.R. Purvis, J.R. Lichtenfels, T.M. Craig, N.O. Dronen, Jr., and N.J. Silvy. 1998. Serologic and parasitologic survey of the endangered Attwater's prairie chicken. *Journal of Wildlife Diseases* 34:137-144.
- Pusateri, F.M. 1990. Greater prairie-chicken recovery plan. Colorado Division of Wildlife, Fort Collins, CO.
- Reijnen, R., R. Foppen, C. Ter Braak, and J. Thissen. 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. *The Journal of Applied Ecology* 32:187-202.
- Rice, L.A. and A.V. Carter. 1982. Evaluation of South Dakota grassland management practices as they affect greater prairie-chicken populations 1974-1978. Completion Report P-R Project W-75-R-(16-21), Study PC-7,1(7509). South Dakota Department of Game, Fish and Parks.
- Rich, T.D., C.J. Bearemore, H. Berlanga, P.J. Blancher, M.S.W. Bradstreet, G.S. Butcher, D.W. Demarest, E.H. Dunn, W.C. Hunter, E.E. Iñigo-Elias, J.A. Kennedy, A.M. Martell, A.O. Panjabi, D.N. Pashley, K.V. Rosenberg, C.M. Rustay, J.S. Wendt, and T.C. Will. 2004. Partners in Flight North American landbird conservation plan. Cornell Lab of Ornithology. Ithaca, NY.
- Ridgway, R. 1873. A new variety of prairie chicken. *Bulletin of the Essex Institute* 5:199.
- Ridgway, R. 1885. Some amended names of North American birds. *Proceedings of United States Museum* 8:354-357.
- Ridgway, R. and H. Friedmann. 1946. The birds of North and Middle America. Part 10. United States National Museum Bulletin Number 50.
- Robel, R.J. 1964. Quantitative indices to activity and territoriality of booming *Tympanuchus cupido pinnatus* in Kansas. *Transactions of the Kansas Academy of Science* 67:702-712.
- Robel, R.J. 1966. Booming territory size and mating success of the greater prairie-chicken (*Tympanuchus cupido pinnatus*). *Animal Behavior* 14:328-331.
- Robel, R.J. 1967. Significance of booming grounds of greater prairie-chickens. *Proceedings of the American Philosophical Society* 111:109-114.
- Robel, R.J. 1970. Possible role of behavior in regulating greater prairie-chicken populations. *Journal of Wildlife Management* 34:306-312.
- Robel, R.J. and W.B. Ballard, Jr. 1974. Lek social organization and reproductive success in the greater prairie-chicken. *American Zoologist* 14:121-128.
- Robel, R.J., J.N. Briggs, J.J. Cebula, N.J. Silvy, C.E. Viers, and P.G. Watt. 1970a. Relationship between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23:295-297.
- Robel, R.J., J.N. Briggs, J.J. Cebula, N.J. Silvy, C.E. Viers, and P.G. Watt. 1970b. Greater prairie-chicken ranges, movements, and habitat usage in Kansas. *Journal of Wildlife Management* 34:286-306.

- Robertson, K. 1980. Changes occurring in Nebraska's prairie grouse range. Pages 52-54 in P.A. Vohs, Jr. and F.L. Knopf, editors. Proceedings of the Prairie Grouse Symposium. Oklahoma State University, Stillwater, OK.
- Rodgers, R., R. Applegate, B. Crouch, R. Ruthstrom, T. Schroeder, K. Sexson, and T. Swan. 2000. Kansas upland game birds - problems and recommended actions. Kansas Department of Wildlife and Parks, Upland Game Bird Initiative Committee.
- Rowan, W. 1926. Comments on two hybrid grouse and on the occurrence of *Tympanuchus americana americana* in the province of Alberta. The Auk 43:333-336.
- Rumble, M.A., J.A. Newell, and J.E. Toepfer. 1988. Diets of greater prairie-chickens on the Sheyenne National Grasslands. Pages 49-54 in A.J. Bjugstad, technical coordinator. United States Department of Agriculture Forest Service General Technical Report RM-159.
- Ryan, M.R., L.W. Burger, Jr., D.P. Jones, and A.P. Wywialowski. 1998. Breeding ecology of greater prairie-chicken (*Tympanuchus cupido*) in relation to prairie landscape configuration. American Midland Naturalist 140:111-121.
- Samson, F.B., F.L. Knopf, and W.R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. Wildlife Society Bulletin 32:6-15.
- Saunders, G.B. 1935. Michigan's studies of sharp-tailed grouse. Transactions of the American Game Conference 21: 342-344.
- Schmidt, F.J.W. 1936. Winter food of the sharp-tailed grouse and pinnated grouse in Wisconsin. Wilson Bulletin 48: 186-203.
- Schmidt, R.A. 1980. Greater prairie-chicken dominated sharp-tailed grouse interaction. Prairie Naturalist 12:13-14.
- Schroeder, M.A. 1991. Movement and lek visitation by female greater prairie-chickens in relation to predictions of Bradbury's female preference hypothesis of lek evolution. The Auk 108:896-903.
- Schroeder, M.A. and R.K. Baydack. 2001. Predation and the management of prairie grouse. Wildlife Society Bulletin 29:24-32.
- Schroeder, M.A. and C.E. Braun. 1992a. Seasonal movement and habitat use by greater prairie-chickens in northeastern Colorado. Colorado Division of Wildlife, Special Report Number 68.
- Schroeder, M.A. and C.E. Braun. 1992b. Greater prairie-chicken attendance at leks and stability of leks in Colorado. Wilson Bulletin 104:273-284.
- Schroeder, M.A. and C.E. Braun. 1993. Partial migration in a population of greater prairie-chickens in northeastern Colorado. The Auk 110:21-28.
- Schroeder, M.A. and L.A. Robb. 1993. Greater prairie-chicken *Tympanuchus cupido*. In: A. Poole, P. Stettenheim, and F. Gill, editors. The Birds of North America, No. 36. The Academy of Natural Sciences, Philadelphia, PA; The American Ornithologists' Union, Washington, D.C.
- Schroeder, M.A. and G.C. White. 1993. Dispersion of greater prairie-chicken nests in relation to lek location: evaluation of the hot-spot hypothesis of lek evolution. Behavioral Ecology 4:266-270.
- Schroeder, M.A., C.L. Aldridge, A.D. Apa, J.R. Bohne, C.E. Braun, S.D. Bunnell, J.W. Connelly, P.A. Deibert, S.C. Gardner, M.A. Hilliard, G.D. Kobriger, S.M. McAdam, C.W. McCarthy, J.J. McCarthy, D.L. Mitchell, E.V. Rickerson, and S.J. Stiver. 2004. Distribution of sage-grouse in North America. The Condor 106:363-376.
- Schroeder, M.A., K.M. Giesen, and C.E. Braun. 1992. Use of helicopters for estimating numbers of greater and lesser prairie-chicken leks in eastern Colorado. Wildlife Society Bulletin 20:106-113.
- Schroeder, M.A., J.R. Young, and C.E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). In: A. Poole and F. Gill, editors. The Birds of North America, Number 425. The Birds of North America, Inc., Philadelphia, PA.
- Schwartz, C.W. 1945. The ecology of the prairie chicken in Missouri. University of Missouri Studies 20, Columbia, MO.

- Sharpe, R.S. 1968. The evolutionary relationships and comparative behavior of prairie chickens. Ph.D. Dissertation, University of Nebraska, Lincoln, NE.
- Short, L.L. 1967. A review of the genera of grouse (Aves, Tetraoninae). American Museum Novitates 2289:1-39.
- Silvy, N.J., C.P. Griffin, M.A. Lockwood, M.E. Morrow, and M.J. Peterson. 1999. The Attwater's prairie-chicken - a lesson in conservation biology research. Pages 153-168 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. The greater prairie-chicken a national look. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Silvy, N.J., M.J. Peterson, and R.R. Lopez. 2004. The cause of the decline of pinnated grouse: the Texas example. Wildlife Society Bulletin 32:16-21.
- Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. Science 236:787-792.
- Soulé, M.E. 1987. Introduction. Pages 1-10 in M.E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge, MA.
- Sparling, D.W., Jr. 1980. Hybridization and taxonomic status of greater prairie-chickens and sharp-tailed grouse (hybridization in grouse). Prairie Naturalist 12:92-101.
- Sparling, D.W., Jr. 1981. Communication in prairie grouse I. information content and intraspecific functions of principal vocalizations. Behavioral and Neural Biology 32:463-486.
- Sparling, D.W., Jr. 1983. Quantitative analysis of prairie grouse vocalizations. Condor 85:30-42.
- Stabler, R.M. and G. C. Miller. 1984. *Plasmodium pedioecetii* in greater prairie-chickens, *Tympanuchus cupido* (Linné), from Colorado. Journal of Parasitology 70:1010-1011.
- Storch, I., compiler. 2000. Grouse status survey and conservation action plan 2000-2004. WPA/BirdLife/SSC Grouse Specialist Group, IUCN, Gland. Switzerland and Cambridge, UK and the World Pheasant Association, Reading, UK.
- Svedarsky, W.D. 1988. Reproductive ecology of female greater prairie-chickens in Minnesota. Pages 193-267 in A.T. Bergerud and M.W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. The Wildlife Management Institute, University of Minnesota Press, Minneapolis, MN.
- Svedarsky, W.D. and R.J. Kalahar. 1980. Female sharp-tailed grouse copulates with greater prairie-chicken in Minnesota. Wilson Bulletin 92:260-261.
- Svedarsky, D. and G. Van Amburg. 1996. Integrated management of the greater prairie-chicken and livestock on the Sheyenne National Grassland. North Dakota Game and Fish Department, Bismark, ND. Jamestown, ND: Northern Prairie Wildlife Research Center home page. <http://www.npwrc.usgs.gov/resource/othrdata/sheyenne/sheyenne.htm> (Version 16JUL97).
- Svedarsky, W.D., R.L. Westemeier, R.J. Robel, S. Gough, and J.E. Toepfer. 2000. Status and management of the greater prairie-chicken *Tympanuchus cupido pinnatus* in North America. Wildlife Biology 6:277-284.
- Svedarsky, W.D., T.J. Wolfe, and J.E. Toepfer. 1999. Status and management of the greater prairie-chicken in Minnesota. Pages 25-38 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. The greater prairie-chicken a national look. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Toepfer, J.E. 1988. The ecology of the greater prairie-chicken as related to reintroductions. Ph.D. Thesis. Montana State University, Bozeman, MT. 533 pp.
- Toepfer, J.E. and R.L. Eng. 1988. Winter ecology of the greater prairie-chicken on the Sheyenne National Grasslands, North Dakota. Pages 32-48 in A.J. Bjugstad technical coordinator. Greater prairie-chickens on the Sheyenne National Grasslands. United States Department of Agriculture, Forest Service General Technical Report RM-159.
- Toepfer, J.E., R.L. Eng, and R.K. Anderson. 1990. Translocating prairie grouse: what have we learned. Transactions of the 55th North American Wildlife and Natural Resources Conference 55:569-579.

- Tompkins, D.M., R.A.H. Draycott, and P.J. Hudson. 2000a. Field evidence for apparent competition mediated via the shared parasites of two gamebird species. *Ecology Letters* 3:10-14.
- Tompkins, D.M., J.V. Greenman, P.A. Robertson, and P.J. Hudson. 2000b. The role of shared parasites in the exclusion of wildlife hosts: *Heterakis gallinarum* in the ring-necked pheasant and the grey partridge. *Journal of Animal Ecology* 69:829-840.
- Toney, T.E. 1980. Foods of greater prairie-chickens on a managed native prairie. Pages 81-84 in P.A. Vohs and F.L. Knopf, editors. *Proceedings of the Prairie Grouse Symposium*. Oklahoma State University, Stillwater, OK.
- U.S. Fish and Wildlife Service. 1993. Attwater's prairie chicken recovery plan. Albuquerque, NM.
- U.S. Fish and Wildlife Service. 2002. Twelve-month administrative finding on petition to list the lesser prairie-chicken (*Tympanuchus pallidicinctus*) as threatened. Ecological Services, U.S. Fish and Wildlife Service, Tulsa, OK.
- Van Sant, B.F. and C.E. Braun. 1990. Distribution and status of greater prairie-chickens in Colorado. *Prairie Naturalist* 22:225-230.
- Vance, D.R. and R.L. Westemeier. 1979. Interactions of pheasants and greater prairie-chickens in Illinois. *Wildlife Society Bulletin* 7:221-225.
- Vodehnal, W.L. 1999. Status and management of the greater prairie-chicken in Nebraska. Pages 81-98 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. *The greater prairie-chicken a national look*. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Walk, J.W. 2004. A plan for the recovery of the greater prairie-chicken in Illinois. Illinois Department of Natural Resources, Springfield, IL.
- Walsh, D.P., G.C. White, T.E. Remington, and D.C. Bowden. 2004. Evaluation of the lek count index for greater sage-grouse. *Wildlife Society Bulletin* 32:56-68.
- Walsh, P.D. 1995. PVA in theory and practice. *Conservation Biology* 9:704-705.
- Washington Department of Fish and Wildlife. 2000. Shrubsteppe mapping of eastern Washington using landsat satellite thematic mapper data. Washington Department of Fish and Wildlife, Olympia, WA. 35 pp.
- Westemeier, R.L. 1971. The history and ecology of greater prairie-chickens in central Wisconsin. College of Agriculture and Life Sciences Resource Bulletin Number 281, University of Wisconsin, Madison, WI.
- Westemeier, R.L. and S. Gough. 1999. National outlook and conservation needs for greater prairie-chickens. Pages 169-187 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. *The greater prairie-chicken a national look*. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Westemeier, R.L., J.D. Brawn, S.A. Simpson, T.L. Esker, R.W. Jansen, J.W. Walk, E.R. Kershner, J.L. Bouzat, and K.N. Paige. 1998. Tracking and long-term decline and recovery of an isolated population. *Science* 282:1695-1698.
- Westemeier, R.L., R.W. Jansen, and S.A. Simpson. 1995. Nest and brood habitats used by translocated greater prairie-chickens in Illinois. Page 17 in J. Kobriger, compiler. *Proceedings of the 21st Biennial Meeting of the Prairie Grouse Technical Council*, Medora, ND.
- Westemeier, R.L., S.A. Simpson, and T.L. Esker. 1999. Status and management of greater prairie chickens in Illinois. Pages 143-152 in W.D. Svedarsky, R.H. Hier, and N.J. Silvy, editors. *The greater prairie-chicken a national look*. Miscellaneous Publication 99-1999, Minnesota Agricultural Experiment Station, University of Minnesota, Saint Paul, MN.
- Wiedenfeld, D.A., D.H. Wolfe, J.E. Toepfer, L.M. Mechlin, R.D. Applegate, and S.K. Sherrod. 2002. Survey for reticuloendotheliosis viruses in wild populations of greater and lesser prairie-chickens. *Wilson Bulletin* 114: 142-144.

- Winter, M. and J. Faaborg. 1999. Patterns of area sensitivity in grassland-nesting birds. *Conservation Biology* 13: 1424-1436.
- Wisdom, M.J. and L.S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. *Journal of Wildlife Management* 61:302-312.
- Yeatter, R.E. 1943. The greater prairie-chicken in Illinois. *Illinois Natural History Survey Bulletin* 22:377-416.
- Zwickel, F.C. 1992. Blue grouse (*Dendragapus obscurus*). *In*: A. Poole, P. Stettenheim, and F. Gill, editors. *The Birds of North America*, Number 15. Academy of Natural Sciences and American Ornithologists' Union, Philadelphia, PA.
- Zwickel, F.C. and M.A. Schroeder. 2003. Grouse of the Lewis and Clark expedition, 1803-1806. *Northwestern Naturalist* 84:1-19.

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